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Behavioral Notes on the Nest-Parasitic Afrotropical Honeyguides (Aves: Indicatoridae)

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ABSTRACT

New data from field studies of Afrotropical honeyguides, examination of label data from specimens in most of the major collections having honeyguides, and review of the literature are bases for updating the biology of Afrotropical honeyguides, last treated by Friedmann (1955). Three species (*Prodotiscus zambesiae*, *Indicator meliphilus*, and *I. narokensis*) have been elevated from subspecific status, and two new species (*Melignomon eisen-trauti*, and *Indicator pumilio*) have been described since 1955. Emphasizing habitat, foraging habits, foods, interspecific behavior, acoustic and visual displays, hosts, and territoriality and breeding habits, new insights are provided into honeyguide biology, although much remains to be accomplished, and the biology of some species is virtually unknown. Honeyguiding habits seem restricted to *Indicator indicator*. At least some honeyguides (*I. indicator*, *I. variegatus*, and *I. minor*) are aggressive about sources of beeswax, with a dominance hierarchy inter- and intraspecifically. Exact pair relations largely remain to be elucidated, but evidence is presented that there is cooperation between individuals, hence extended pair

bonds, assisting female honeyguides to enter well-defended nests of their hosts. Some Lesser Honeyguide (*I. minor*) males seek out duetting pairs of their barbet hosts, monitor them, and defend them against conspecific male honeyguides. Honeyguides parasitizing barbets monitor barbet activities about the barbets' roosting or nesting holes even in the nonbreeding periods. A nestling honeyguide (*I. minor*) was seen making its initial departure from its host's (*Stactolaema anchietae*) nest; a host barbet arriving to feed it shifted recognition from that of a (foster) nestling to that of a "honeyguide," and immediately and violently attacked the young honeyguide, which was driven out of the barbets' territory. Young honeyguides essentially must be able to fend for themselves when they exit from the nest. The destruction of the host's eggs or young, by the laying female honeyguide or later by the young honeyguide, is important to insure that the nestling honeyguide secures maximum feeding. The same Lesser Honeyguide situation involving that nestling provided evidence of continual monitoring of the nest by one and sometimes two Lesser Honeyguides

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right up until the fledging of the young honeyguide. The sight and sound of adult honeyguides thus may be familiar to a young honeyguide even before it leaves the hosts' nest. New vocal and visual displays are described for a number of honey-

guides. For the sake of completeness, full lists of honeyguide hosts are provided for each species, and the information provided effectively summarizes what is known of Afrotropical honeyguides in 1984.

INTRODUCTION

The honeyguides (Indicatoridae) include approximately 17 species of four genera distributed in tropical Africa (the Afrotropics, a now widely accepted term for sub-Saharan Africa) and tropical Asia. Only two species of one genus (*Indicator*) are Asian, the other species of that genus and the other three genera being endemic to Africa. These piciform birds are known especially for their honeyguiding habit, and for their nest parasitism of other birds. In fact, these are little known birds, with most published information dealing with honey-guiding, which is actually proven for only one species (*Indicator indicator*), and with details, some speculative or circumstantially derived, on hosts of these parasitic birds. The most recent treatment of the family is that of Friedmann (1955). Since that publication, scattered information has been published by Friedmann (1958, 1958a, 1963, 1968, 1969, 1970, 1978a, and 1978b), and there have been notes in diverse journals but few (e.g., Chapin, 1958, 1962; Colston, 1981; Louette, 1981; Prigogine, 1978; Roberts, 1956; and Short and Horne, 1979, 1983) that contain many details about honeyguides.

Our purpose here is to provide information on the biology of Afrotropical honeyguides, summarizing the scattered published details, and adding new information on species that we have studied since 1976. Some of this new information raises questions about the feeding habits, aggressiveness, territoriality, and other aspects of honeyguide behavior as presented earlier by Friedmann (1955), and as generally accepted in the ornithological literature about this interesting group of birds. This report supplements and updates Friedmann's treatise, without duplicating its descriptions and other information.

We stress that the honeyguides are incompletely known, generally because individual birds cover large areas, fly rapidly, and concentrate their feeding at beeswax or other sites

over short periods of time. Honeyguides are drably colored, generally inconspicuous birds. Their nest parasitism often involves hole-nesting species, and the presence of honeyguides in the nests of foster parents often goes undetected by human observers. No one, for example, knows what terminates the young honeyguides' relations with the foster parents (but see below, under *Indicator minor*).

LOCATION OF FIELDWORK

Field studies have taken place during diverse times of the year in Kenya in all years from 1976 to the present. Study sites have regularly included Kakamega Forest, Chesumot Farm near Kericho, Ol Ari Nyiro (Laikipia Ranching Company, on the Laikipia Plateau), the Kedong Valley, Karen, Olorogesailie National Prehistoric Site, the Loita Plains and Narok region, and the coastal, threatened Arabuko-Sokoke Forest on numerous occasions. Other sites have included: the Endebess region and slopes of Mount Elgon in December 1982; the Lake Magadi region and southern Ewaso Nyiro River in January 1983; the north (Kenyan) slope of Mount Kilimanjaro in November 1982; Narosura, the Lenkutoto Plateau, and the upper southern Ewaso Nyiro River in July 1979; the northwestern Mau Forest in October and November 1976; the Naro Moru region in March 1976; the area around Ngobit and Nyeri in October 1976; the Loldaika region, Maralal, and the area about Barsaloi in October 1976; Lewa Downs in July and August 1977; Lake Baringo and Tangel Bei in August 1977; the Narok-Mosiro region in July 1978; the Shimba Hills in August 1978; Diani Beach, the remnant Jadini Forest, and Shimoni in November 1981; the area about Mount Suswa in November 1980; the Kapsabet-Muhuroni region in September 1980; the area about Koru, the Nandi Scarp, and Chemelil in De-



FIG. 1. Study site of beeswax experiments, Ol Ari Nyiro Ranch, central Kenya, December 1983. Open riverine acacia woods (*Acacia xanthophloea*), with surrounding slopes in mixed dense acacias and other trees, elevation about 1770 m.

cember 1981; the Chyulu Hills in November 1982; and the Ngulia region of Tsavo West National Park in July 1977. We also have made study visits to Amboseli, Masai Mara, and the Aberdare national parks, as well as studying sporadically along roads throughout western, central, and southern Kenya, and coastal Kenya north to the mouth of the Galana River. Horne has studied birds in Africa for three decades, and has made observations on honeyguides throughout Kenya (e.g., the Lake Turkana region, the Tana River, Marsabit, Lake Jipe, Kisii, the Ngurumans, Kulal, and elsewhere, and on frequent occasions in Uganda, Tanzania (where she lived for ten years), Zaire, and Ethiopia. Short has observed honeyguides in Cameroun and South Africa, and both authors studied them in Akagera Park, Rwanda, in early January 1982; in northern, central, and western Malawi during August and September 1980; and in the Ndola and Choma regions of Zambia in October and November 1983.

METHODS AND MATERIAL

Observations were made with 8 to 10 power binoculars, and notes were taken by writing, and at times on tape recorders, as the observations occurred. Vocalizations were recorded by Horne on a Stellavox SP-7 recorder, generally with a 72 cm parabolic reflector, and a Schoeps CMC-45 microphone. Playback was by Short using a Sony cassette recorder. Audiospectrographic analysis was with use of the Ornithology Department's Kay Elemetrics Sonagraph 6061B, using wide-band filter.

Experiments were conducted on Ol Ari Nyiro in December 1983, using commercial "brown honeycomb" (a mixture of broken beeswax from honeycombs, dried particles of honey, and pieces of larvae and other stages of bees) and pure, transparent, white to brownish honeycomb obtained from an abandoned bees' nest in an elephant-felled tree by Stephen Njugai. These two materials were placed at opposite sides of an emptied



FIG. 2. Insertion of beeswax into abandoned, cut-out (by honey-gathering people) hive, below central large acacia in fig. 1, by field assistant Stephen Njugai. This and all following photographs (except fig. 4) were taken at Ol Ari Nyiro, Kenya, in December 1983.

beehive in an *Acacia xanthophloea* tree; the abandoned hive had been cut open and the honey removed at least several months previously by human honey-gatherers (figs. 1–3). On ten days we made the two materials available to local honeyguides *ad libitum* for from 3 to 6 hours a day within that opened hive, the two sides being 25 cm apart. The results of the experiments are described below.

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Paolo Gallman and Mr. and Mrs. Colin Francombe greatly assisted our studies on Ol Ari Nyiro. Ann and Pat Donnelly helped us, and hosted us in coastal Kenya. Iris and Sandy Wilson in Malawi, Jean-Pierre Vande weghe in Rwanda, and Margaret and Paddy Bruce-Miller, Loretta and Clide Carter, Dylan Aspinwall, and Robert Stjernstedt in Zambia gave us a great deal of assistance. We also thank Cecilia Muringo, Claude Chappuis, Joseph Mwaki, Lorio Lukiro, Michael Webley, Anna and Karl Merz, John Wilson, Isobel Bennett, Sybil Sassoon, Mulji Modha, Anna and Chris Obura, J. Colebrook-Robjent, and many others who helped us in the field, including many game wardens and forestry officials.

Herbert Friedmann kindly commented on a version of this manuscript, benefiting it greatly. Anthony Diamond contributed unpublished observations on *Indicator indica-*



FIG. 3. The abandoned hive of figure 2. Pure honeycomb was placed at the far (left) end, and "brown" comb (broken comb with honey and bee fragments) was placed at the near (right) end, just inside the "lip" of the hive entrance.

tor, for which we are greatly obliged. G. R. Cunningham-van Someren made helpful suggestions regarding the manuscript, and identified some stomach contents, for which we thank him.

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SPECIES ACCOUNTS

The accounts that follow are in the systematic framework provided by Snow (1978), which we follow very tentatively, for we feel that taxonomic problems are numerous in this family. Indeed, almost a quarter of the species now recognized have been elevated

to species or described as new within the past quarter century, the latest being *Melignomon eisentrauti* (Louette, 1981). We have field experience with all the Afrotropical species except *Prodotiscus insignis*, *Melignomon zenkeri*, *M. eisentrauti*, and *Indicator willcocksi*. Nonetheless, we treat all species—for the sake of completeness and because data on each species affect the interpretation of data available for all other species.

Detailed descriptions and discussions of systematics are to be covered elsewhere (Short and Horne, in prep.), and we assign subspecies based on geographical reasons unless we state our other reasons for so designating them. For each species we treat: range summary, habitat, foraging habits, foods, interspecific behavior (unrelated to nest-parasitism), acoustic displays, visual displays, hosts, and territoriality and breeding habits. Our concentration is on recently acquired information. Older information is either covered

by citations or mentioned in detail only for the sake of clarity.

GENUS *PRODOTISCUS* SUNDEVALL

These birds are best called "honeybirds," as they certainly do not "guide" to honey sources. Their hosts are diverse, including many that are not hole-nesting species. Thus, honeybirds are the only piciform birds not closely associated with cavities or holes in trees. They are inconspicuous, their voices are little known, and few observers have noted them more than casually. They have a fine, sharp bill, which differs from the stubbier, heavier bill of most other honeyguides; but they share with the others white outer tips of the tail. White flank patches of feathers that are erected in certain displays are characteristic.

Prodotiscus regulus Sundevall Brown-backed Honeybird

RANGE SUMMARY: It occurs disjunctly in West Africa about Mt. Nimba in Guinea, in Togo, and from eastern Nigeria to western Central African Republic; farther east in east-central Sudan to central and southern Ethiopia; and from southern Uganda and central Kenya southward circling the Congo forest in Rwanda, Burundi, and Tanzania, and from Angola and southern Zaire south to northern Namibia, Botswana, Transvaal, eastern Cape Province, and Natal. Southern African populations may be partly migratory.

HABITAT: This honeybird frequents very diverse woodlands, even entering exotic (Australian) acacia plantations, the edges of riparian forest, grasslands with scattered trees or thickets, dense thorn scrub, and orchards and gardens. It avoids deserts and dense, wet forests, but flies across open country without trees, perching occasionally on grass stalks. Within woodlands it seems to occur in the understory and in smaller trees more often than in the canopy, which the less frequently observed *P. zambesiae* seems to favor. It is found from sea level to approximately 2000 m elevation (Kenya, Cameroun), perhaps generally not reaching such high elevations in southern Africa.

FORAGING HABITS: The usual feeding mode is by gleaning on twigs amid leaves and on

branches, creeping over the bark, but it also flycatches from a perch and hovers before flowers to obtain insects. Sometimes it is found low in grass (Benson and Stuart Irwin, 1967) or flowers in gardens. It forages with flocks of white-eyes (*Zosterops* spp.) and tits (*Parus*). There are reports that it occasionally enters cavities, but whether to forage or to seek hosts' nests is uncertain (see Friedmann, 1955, p. 260).

FOODS: This is primarily an insectivorous species, eating aphids, lepidopterous and coleopterous larvae, and especially scale insects (Coccidae), but it also takes flying insects of unknown species. Some feeding occurs on *Loranthus*, possibly for scale insects. Stomachs often contain the waxy exudate of scale insects, and beeswax itself has been reported (Friedmann, 1955), although the bird is not known to visit beehives.

INTERSPECIFIC BEHAVIOR: Except for flocking behavior noted above, and behavior relating to possible hosts, there are no data.

ACOUSTIC DISPLAYS: Known calls include: a scream uttered in distress by a wounded individual; a chattering call; a single "zeep" or a double "zeep-zeep" that is the main call given in flight; a buzzy, strident note; a sibilant "zzzz" reportedly uttered in courtship; and a supposed song, a "tseeu tseeu" (Friedmann, 1955, p. 261) by a subadult female that flipped its tail and spread it, showing the white outer tips.

VISUAL DISPLAYS: The tail movements of a singing subadult female are mentioned above. An apparent aggressive display involves the erecting of the white flank feathers to form conspicuous patches, used against a host species, *Petronia supercilialis*. When perched and foraging it makes distinctive *side-to-side* movements of the head, rather as if focusing visually on something, but the behavior is conspicuous and species-specific (see *P. zambesiae*). These movements likely are a display. The tail frequently is spread when the birds are perched or flycatching; the spread tail is an aggressive display generally in honeyguides. In apparent courtship (or possibly an aggressive encounter), two birds pursued one another, calling "zeet-zeet," then perched 25 cm apart; one then drooped its wings, fluffed its body (especially flank feathers), and, spreading its tail, leaned forward and called

“zzzz”—the second bird called “zeep” and flew, seemingly pursued by the first.

HOSTS: This honeybird is known to parasitize the finch *Petronia superciliaris*, and the warblers *Camaroptera brachyura* and *Cisticola fulvicapilla*. It has been noted near other cisticolas, and these may prove to be the major hosts. Brown-backed Honeybirds have been seen emerging from nests occupied by the swift, *Apus horus*, and from nesting cavities of the Pied Starling (*Spreo bicolor*). Whether these species are parasitized, or the honeybirds were seeking insect food in those nests, is uncertain. This honeybird has been seen being chased by pairs of *Petronia superciliaris*, *Cisticola rufilata*, and *Nectarinia senegalensis*; these are known (*Petronia*) or prospective hosts.

TERRITORIALITY AND BREEDING HABITS: There is no knowledge of territoriality and pairing. So sparse are data that we have singing only from a young female,³ and “courtship” noted that may in fact refer to an agonistic encounter. Two birds, presumed to be male and female, have been observed together for periods of time while feeding, suggesting that pair relations may involve more than a brief meeting for copulation. Data from specimens indicate that a female may lay five eggs or more. Breeding generally is in October to March in southern Africa, and at diverse times (e.g., March, May, October in Zaire) not forming any pattern farther north. Observations suggest that the hosts raise only one honeybird in a parasitized nest, hence that the adult female honeybird, or the young bird punctures eggs or kills the young of the host.

Prodotiscus insignis (Cassin)
Cassin's Honeybird

RANGE SUMMARY: This honeybird, forming a superspecies with the more eastern and southern *P. zambesiae*, inhabits West and Central Africa from Liberia and Sierra Leone east through southern Nigeria and southern Cameroun to northern Zaire, southeastern Sudan, and Uganda to western Kenya, and

south to northern Angola in the west, and northeastern Zaire and southern Uganda in the east (Snow, 1978). There are no records from coastal West Africa west of southern Nigeria, and it is missing from large areas of central Zaire.

HABITAT: From the gaps in its range in West Africa and in central Zaire, we suggest that, although a forest species, this honeybird favors clearings and forest edges rather than dense forest (see also Friedmann and Williams, 1971). It is found in second-growth, and in tall trees scattered above coffee plants, as well as in small trees at the edges of forest. It has been found from sea level to 1200 m in Angola and Zaire, and up to 2200 m in western Kenya and Uganda (Britton, 1980).

FORAGING HABITS: This honeybird flycatches for insects from a perch, or flutters or climbs from branch to branch, gleaning insects in the manner of species of *Parus*. Occasionally it joins mixed species foraging flocks, in numbers up to three (usually only one, or two).

FOODS: It eats dipteran and hymenopteran insects, and probably numerous others. Some unidentified fruits have been reported (on labels) in stomach contents. Wax also has been noted on labels, but whether of insects' exudates or bees is uncertain.

INTERSPECIFIC BEHAVIOR: Unknown, except as related to flocking (above) or hosts (below).

ACOUSTIC DISPLAYS: Various chattering notes and weak “whi-kiki” calls have been reported (Friedmann, 1955, p. 251).

VISUAL DISPLAYS: Except for tail spreading displays as it flies in foraging, no displays are known.

HOSTS: There are no absolutely certain records of hosts of this honeybird, although it is reported or assumed to parasitize white-eyes (*Zosterops* spp.), flycatchers (Muscicapidae), and warblers of the genus *Apalis* (see Friedmann, 1955, pp. 251–252).

TERRITORIALITY AND BREEDING HABITS: Data are lacking on territoriality and hosts. Individuals have not been followed in any reproductive setting. Peculiarly, Brosset (1981) has reported feeding of a juvenile of this species by an adult Cassin's Honeybird, the only such instance of possible parental care known in the honeyguides. Breeding

³ We heard L. Gillard's recording of 2–3 second trilling song in 1985, and used it to elicit and tape-record such songs in Kenya, from likely males.

dates are based upon adult female specimens with well-developed eggs in the ovary or oviduct. These suggest November breeding in Cameroun, January in Sudan, July in Uganda, March in Kenya (Brown and Britton, 1980), July in Zaire, and September in Angola.

Prodotiscus zambesiae Shelley
Green-backed Honeybird

RANGE SUMMARY: This uncommon honeybird replaces *Prodotiscus insignis*, its close relative, in eastern and southern Africa. It was considered conspecific with *P. insignis* by Friedmann (1955), but now generally is treated as a separate species (e.g., Snow, 1978; Britton, 1980). The Green-backed Honeybird occurs from west-central Angola, northern Zambia, southeastern Zaire, and southern Tanzania south to northeastern Namibia, Zimbabwe, and southern Mozambique. Local, apparently somewhat disjunct populations also occur in west-central Ethiopia, in central and southern Kenya, and in northeastern Tanzania (Snow, 1978).

HABITAT: It frequents woodlands, forest edges and clearings, riparian woods, and gardens and other cultivated areas. In central Africa it reaches 2130 m and it usually is found above 900 m in East Africa (Britton, 1980); farther south it extends from sea level to 1400 m in Angola, 1200 m in Zimbabwe, and 1670 m in Malawi. Its erratic presence in places in Kenya (e.g., Karen, personal observation) and elsewhere suggests local movements, although this has not been established.

FORAGING HABITS: The Green-backed Honeybird forages like a slow-moving sylviid warbler, except that it frequently perches quietly and then sallies from the perch to seize insects in the air. It often *bobs* its head when perched (see *P. regulus* above). We have seen it creep about the bark and leaf clusters, probing into mosses and lichens, and taking scale insects off petioles of leaves. When it shifts to flycatching its flight often is showy, with a flair caused by the spread, fully white outer tail tips; rather than directly taking the insect and returning to a perch, it may circle, zigzag, or flutter to one side, then go on to another perch. Although it often frequents the canopy of trees when foraging, we have seen one feed-

ing for two hours at 2 to 15 m, mainly at 5 to 10 m above the ground in a jacaranda tree, a fever tree, and in rose bushes in our Karen, Nairobi, garden, appearing to feed on two consecutive days at the same sites and times (13:00 to 15:00 hours). Occasionally this bird preened, drooped its wings in sunning itself, and scratched its head (under the wing) with its feet. It often bobbed its head when not gleaning with some movement to the side as well (hence its difference from *P. regulus* in head movements is only in the up-down component), as if peering at something, although we noted no obvious object of such scrutiny. This honeybird sometimes joins mixed foraging flocks of sylviid warblers, Campephagidae (cuckoo-shrikes), Pycnonotidae (bulbuls), Zosteropidae (white-eyes), and ploceid finches. These flocks may contain two or rarely three Green-backed Honeybirds, and sometimes Brown-backed Honeybirds occur in the same foraging flocks.

FOODS: It feeds chiefly on spiders and insects, including scale insects and their waxy exudate, termites, beetles, bugs (Homoptera), moths, and flies. Stomach contents also mention undetermined seeds and *Loranthus* berries.

INTERSPECIFIC BEHAVIOR: This honeybird occasionally attacks tits (*Parus* spp.) and some other small birds, with which it may occur in mixed foraging flocks. No interactions have been noted with *Prodotiscus regulus*, although the latter has been seen in foraging flocks with it.

ACOUSTIC DISPLAYS: Calls reported from this species are a chattering series, a note "fit," a flight call "skeee-aaa" apparently uttered during courtship (Friedmann, 1955, p. 251), and a likely song, "pee-eee-it" (Short and Horne, 1979, pp. 3-4). The song was given repeatedly from a perch in the woodland of coastal Kenya. Playback of the call, which consists of a low "pee," followed by a whistly rising "eee," and then a sharp clicking "it," caused the caller to move about excitedly, spreading its tail, and answering with the same call. In Karen, Kenya, playback of this "song" to a nonvocal Green-backed Honeyguide caused the latter to cease feeding, approach the source of the sound, and hop about with its tail repeatedly spread and shut (but it did not call).

VISUAL DISPLAYS: The head bobbing of this

distinctly small-headed species, with occasional side-to-side movements, may be a species recognition display enabling a mate or other conspecifics to maintain contact. (In shade the Green-backed Honeybird looks and acts much like the flycatcher *Muscicapa adusta*.) One honeybird was reported to approach another, bobbing its head up and down and spreading its conspicuous white flank patches, before both flew (Friedmann, 1955, p. 250, reporting J. G. Williams' observations). Benson and Benson were cited by Friedmann (*loc. cit.*) as seeing an individual in flight over the trees while calling ("skeee-aaa") at intervals of once per second, possibly a courtship flight display. Begging young droop their wings and show their orangish gape as they follow their foster parents about.

HOSTS: The major hosts appear to be species of white-eyes (*Zosterops abyssinica*, *Z. polio-gastra*, and *Z. senegalensis*), with which it often can be seen foraging. It also is known to use the Amethyst Sunbird (*Nectarinia amethystina*) and the Black-throated Wattle-eye (*Platysteira peltata*), a flycatcher (Friedmann, 1958a). G. R. Cunningham-van Someren also reports having seen Dusky Flycatchers (*Muscicapa adusta*) and Paradise Flycatchers (*Terpsiphone viridis*) used as hosts by this honeybird. One seen at a hole in a tree occupied by a pair of Southern Black Tits (*Parus niger*) may have been foraging, and literature reports of tinkerbirds (*Pogoniulus* spp.) and rock-sparrows (*Petronia* spp.) as hosts are unsubstantiated (Friedmann, 1955). All of the known hosts build cup-shaped nests. We have noted one Green-backed Honeybird flycatching about a pair of Montane White-eyes (*Zosterops polio-gastra*) that were gathering nesting material.

TERRITORIALITY AND BREEDING HABITS: Other than some indications of aggression in displays, there are no data on territoriality or pair formation. Definite egg dates are from April to July, December, and February, all during or after rains in Kenya and northern Tanzania, and August to October in Zimbabwe (Stuart Irwin, 1981). The juvenal honeybirds fed by foster parents are unaccompanied by young of the hosts (inferring destruction of the host's eggs or young by the honeybirds), although van Someren (1956) found two young of *P. zambesiae* in one nest of *Zosterops*.

GENUS *MELIGNOMON* REICHENOW

These small honeyguides are very little known, one being described only recently (Louette, 1981). They combine a thin bill, feeding habits, and morphology, including a thick gizzard, and deep sternal notches of *Prodotiscus* with the thick skin, greater number of tail feathers (12), coarser plumage, and slit nostrils of *Indicator*. The sternal keel is intermediate between that of these two genera.

Melignomon zenkeri Reichenow Zenker's Honeyguide

RANGE SUMMARY: A rare forest bird, Zenker's Honeyguide occurs in southern Cameroun and adjacent Rio Muni, and farther east from the southeastern Central African Republic to northern and northeastern Zaire and the southwestern corner of Uganda (Friedmann, 1968).

HABITAT: It is known to occur in lowland forest, reaching into the highlands of eastern Zaire to an elevation of 1530 m about Lake Kivu.

FORAGING HABITS: These are likely to be like those of species of *Prodotiscus* to some extent (see foods, below) but observations are lacking.

FOODS: Contents of stomachs include scale insect (Coccidae) pupae, emerging adults and cocoons, and gray waxy material mixed with insect fragments (Friedmann, 1968), probably from scale insects rather than wax from beehives.

INTERSPECIFIC BEHAVIOR, ACOUSTIC DISPLAYS, AND VISUAL DISPLAYS: Unknown.

HOSTS: Its hosts are unknown. Barbets have been suggested but the similarity of this honeyguide's foods to those of species of *Prodotiscus* equally suggests that it may use warblers, flycatchers, or other hosts of groups used by other honeybirds of that genus.

TERRITORIALITY AND BREEDING HABITS: The sparse data on breeding are gleaned from specimens. A juvenile taken in March in Cameroun suggests January and February breeding. A Bwamba, Uganda, female had two ova well developed and a third enlarging in July. A Central African Republic female taken in June had ova somewhat enlarged. Prigogine (1971) and others have suggested

breeding during the January to March rainy period in eastern Zaire, but it also appears to breed about Lake Kivu in (dry) August.

Melignomon eisentrauti Louette
Eisentraut's (or Coe's) Honeyguide

RANGE SUMMARY: This honeyguide apparently is rare, being known from the area around Mt. Nimba, Liberia, and in southwestern Cameroun (Louette, 1981; Colston, 1981). It also may occur in Ghana (Macdonald, 1980). This taxon appears to represent a valid species that forms a superspecies with *M. zenkeri*, from which it differs in its more olive-yellow dorsum, grayer ventral surfaces, and whitish posterior underparts.

HABITAT: Specimens have been obtained in wet primary forest and in secondary forest, and it occurs likely in lowland forests generally in parts of West Africa where such forest remains.

FORAGING HABITS: It forages somewhat like sylviid warblers in the middle and upper parts of forest trees, according to Colston (*in litt.*). See related *M. zenkeri*.

FOODS: Stomachs examined contained "insects," yellow "wax" or possibly pollen, seeds, and small fruits (Colston, 1981).

INTERSPECIFIC BEHAVIOR, ACOUSTIC DISPLAYS, AND VISUAL DISPLAYS: None reported.

HOSTS: Not known, suggested as possibly woodpeckers (*Campethera caroli*, *C. nivosus*, breeding condition at same time as *M. eisentrauti*, but, if like *Prodotiscus* in foraging, could be parasitic on other than picids).

TERRITORIALITY AND BREEDING HABITS: A March female from Mt. Nimba was in breeding condition, and molting adults suggest that breeding occurs there between November and June, and a December female from Mt. Cameroun, with an enlarged ovary may have been preparing to breed (Louette, 1981). There is no positive indication of hosts.

GENUS *MELICHNEUTES* REICHENOW

This monotypic genus, doubtfully distinct from *Indicator*, is characterized by a sternum deeper than that of *Indicator* and highly modified (derived) central two pairs of tail feathers (Chapin, 1939, p. 554). The tail features in a remarkable flight display, with sound likely produced by the air moving through it.

Melichneutes robustus (Bates)
Lyre-tailed Honeyguide

RANGE SUMMARY: Because it is conspicuous mainly when in flight, and thus difficult to collect, this honeyguide is very little known, but its distinctive display sounds give us knowledge of its occurrence in areas from which we lack specimens. It occupies forests in the Mt. Nimba region of Guinea and Liberia, and from southeastern Nigeria east to the southern Central African Republic and formerly southwestern Uganda, thence south to northwestern Angola and south-central and eastern Zaire.

HABITAT: It is reported from forests and forest edges, and also secondary forest, cleared areas in forest, and coffee plantations (Friedmann, 1978b). Although a lowland species, it reaches 2000 m elevation in eastern Zaire.

FORAGING HABITS: It is known to flycatch for insects in the air (Chapin, 1939), and it forages about beehives. Most information comes from native collectors who find them about bees' hives. It usually frequents the canopy but several have been collected in mist nets within a meter or two of the ground (Friedmann, 1978b). There are no reports of its guiding animals to honey sources.

FOODS: From stomach contents, it is known to eat beeswax, spiders, and undetermined insects.

INTERSPECIFIC BEHAVIOR: Unknown.

ACOUSTIC DISPLAYS: The vocalizations and mechanical sounds are surprisingly well known, and indeed are the main factor contributing to detection of the presence of this honeyguide. A purring note uttered in flight, a harsh call, a chatterry "tarara-tarara-tarara-," and a buzzy low "ny, ny" are known calls, without ascribed function. The display flight sounds for which the species is remarkable were rendered "nyete-nyete-" by Chapin (1939), and usually called nyete sounds or calls. Recordings of this by C. Chappuis that we have heard (see Chappuis, 1981) are of honking or tooting series starting as single, then giving way to double notes that may be rendered "eh, eh, eh, eh-eh, kua, kua, kua, kua-but, kua-but, kua-bu, kua-bu, kua-bu, eee-eh." The end of the "call" almost is that of a braying, although it sometimes ends in a loud "wow-wow-wow!" There is an in-

crease in tempo and volume through the series. Observers indicate that the sound is produced by the honeyguide when plummeting downward in a spiral or zig-zagging flight.

VISUAL DISPLAYS: The display flight, acoustic aspects of which are described above, consists of a honeyguide flying to a considerable height over a forest during one or two minutes, then dropping rapidly over about 30 seconds, giving forth the sounds described above. The sounds likely are produced by the tail feathers that are modified in both sexes. Friedmann (1978b) feels that the reports of this display essentially indicate that it occurs year-round. Its function is unclear, but the flights occur in proximity to feeding areas, and they could be territorial, or be involved in pair formation or pair maintenance. Two birds do not usually display at the same time, nor does a flight display elicit responses from other individuals.

HOSTS: These are at present unknown, although Friedmann (1978b) and others (e.g., Rougeot, 1950) suspect that it parasitizes species of the forest barbets of the genus *Gymnobucco*, one or more of which occur throughout the range of *M. robustus*.

TERRITORIALITY AND BREEDING HABITS: Nothing is known of its territoriality, if indeed it is territorial. Flight displays appear to be not closely tied with territoriality. Breeding data come chiefly from the condition of gonads in adult specimens. One nestling is known (Friedmann, 1978b, p. 651), but its host's nest was not identified! It was taken during April in northeastern Zaire. Specimens of adults with enlarged gonads represent April and August in eastern Zaire, and June in the Central African Republic (Friedmann, 1978a).

GENUS *INDICATOR* STEPHENS

The largest genus of the family, *Indicator* includes the largest and smallest species, and is the only genus represented outside Africa (in southern Asia). Slitlike nostrils, a generally sturdy bill, thick skin, 12 rectrices, a tufted oil gland, a thin-walled ventriculus, and a narrow keel of the sternum mark these species. Guiding of mammals to beehives is known for one species (*I. indicator*) conclusively, and suggestive evidence requiring confirmation is

available regarding occasional guiding by *I. variegatus*. All other species that are reasonably well known, as well as those that guide, feed to some extent upon beeswax. Considerable uncertainty obtains concerning the status of taxa of the small- and medium-size members of the genus. We are not as yet prepared to comment in depth upon the taxonomy of these honeyguides (a preliminary manuscript is in preparation). However, we do arrange the species in a unique classification, based upon the clearly derived honeyguiding habits, and sexual dimorphism of the *indicator* species group (*I. maculatus*, *I. variegatus*, *I. indicator*) of large-size honeyguides.

Indicator willcocksi Alexander Willcock's Honeyguide

RANGE SUMMARY: This species is known from Guinea-Bissau, Liberia, Ghana, and western and central Nigeria eastward through Cameroun and southern Central African Republic to southwestern Sudan, and southward to northern and eastern Zaire, and western Uganda. It probably occurs in Ivory Coast and other West African countries, but is often mistaken for other small honeyguides, especially *I. exilis*.

HABITAT: It is known as a forest bird of the lowlands but its distribution and some observations suggest that it actually prefers forest clearings and edges, riverine forest in open country, and dense wooded patches in grasslands. It occurs up to 1800 m in Zaire and Uganda, usually below 1500 m (and below sympatric *I. pumilio*) in eastern Zaire, but between 1200 and 1800 m in western Uganda.

FORAGING HABITS: This little known honeyguide flycatches for insects from a perch, and gleans in the foliage of dense trees.

FOODS: These include flying ants, lepidopterous (moth) larvae, other "insects," beeswax, and wax of unknown origin, possibly exudates of insects.

INTERSPECIFIC BEHAVIOR: Unknown.

ACOUSTIC DISPLAYS: The only tape recordings of its calls are of its song (Chappuis, 1981). This is characterized by a sharp, mechanical snapping sound at the end of each three-parted note, and the lack of a distinct

tive initial note (found in related species *I. exilis* and *I. minor*). From Chappuis' recordings, which we have heard, the song can be described as a "p-will (snap), p-will (snap), pe-will (snap), pe-weel (snap), -." The notes peak at about 2.5 kilohertz on their second element and end in a snapping sound at 2–5 kilohertz. We have played back copied songs of this species in central Kenya, eliciting identical replies, but so far have been unable to determine the identity of the singer (unpublished notes). Prigogine (1971, p. 105) reported its vocalizations the same as those of *I. pumilio*; although it is uncertain which vocalizations he meant, it is unlikely that two sympatric honeyguides would be vocally alike, and nothing like the above song of *I. willcocksii* has been noted for *I. pumilio*.

VISUAL DISPLAYS: Unknown.

HOSTS: Unknown.

TERRITORIALITY AND BREEDING HABITS: It is known to sing, presumably territorial songs, but data are almost nonexistent. Breeding as determined from the size of gonads of adults is in: August and September about Mt. Nimba; February in Ghana; January, February, and May in Nigeria (Elgood, 1982); January and February in Cameroun; and February, April, June, and September in Zaire (also Zaire juveniles in February and April).

Indicator pumilio Chapin
Dwarf Honeyguide

RANGE SUMMARY: This honeyguide occupies the highlands of northeastern Zaire, adjacent Rwanda and Burundi (Vande weghe, *in litt.*), and the Impenetrable Forest of western Uganda. Occurrences elsewhere are suspect because of confusion with other small honeyguides, especially *I. willcocksii* and *I. exilis* (Prigogine, 1978).

HABITAT: It occurs in montane forests at elevations from 1500 to 2400 m, usually above 1500 m, and at an altitude usually greater than that of *I. willcocksii*.

FORAGING HABITS: This inconspicuous honeyguide was discovered only in the 1950s by Chapin (1958), and its habits are little known. It mainly has been observed feeding on pieces of honeycomb put out to attract honeyguides, in the company of *I. exilis*.

FOODS: Stomach contents are reported only as beeswax and "insects."

INTERSPECIFIC BEHAVIOR: Although collected with *I. exilis* at honeycomb sites (Chapin, 1958, 1962), its behavior with regard to that species has not been described.

ACOUSTIC DISPLAYS: Its calls are essentially unknown. A "tuutwi" call was reported by Prigogine (1971) to be different from calls of *I. exilis*, but with no discussion or indication of function.

VISUAL DISPLAYS: Unknown.

HOSTS: Unknown.

TERRITORIALITY AND BREEDING HABITS: The only available data on its breeding come from eastern Zaire specimens, namely of juveniles in June, August, and October, immatures from December and January, and adults in breeding condition from May to October. Prigogine (1971) reported breeding about Lake Kivu in April.

Indicator narokensis Jackson
Kilimanjaro Honeyguide

RANGE SUMMARY: We caution that this honeyguide is unlikely to be distinguished in the field from *I. meliphilus*. Contrary to descriptions by Forbes-Watson (1977) both species have a loreal mark, and seasonal variation in plumage coloration is so great that one cannot rely upon "greener" versus "gray-er" appearance of, respectively, *I. meliphilus* and *I. narokensis*. From specimens, the Kilimanjaro Honeyguide occurs from the eastern edge of Uganda across central Kenya to southern Kenya (reaching woodlands near the coast), and probably adjacent northern Tanzania.

HABITAT: It frequents dry woodlands, scrub woodlands, and wooded grasslands, including streamside vegetation in dry bushland, at elevations from near sea level to 1800 m.

FORAGING HABITS: This honeyguide is known to flycatch for insects from low to high perches in the canopy. It also forages for beeswax at bees' nests. Insect foraging is conducted at all heights in trees and in bushes.

FOODS: Details from specimen labels indicate beeswax, scales (likely scale insects), other unspecified insects, and undetermined fruits.

INTERSPECIFIC BEHAVIOR: Suspected hon-

eyguides of this species (Short and Horne, 1979) interacted with individuals of *Indicator minor* and were chased away by, or fled from, calling *I. minor* in Arabuko-Sokoke Forest, Kenya. It seems attracted by the activities, including calling, of *Indicator minor*, although it is submissive to that species and usually moves away after quietly approaching the position of calling Lesser Honeyguides.

ACOUSTIC DISPLAYS: These are known only from uncollected small honeyguides believed to be of this species (because of color pattern; specimens of it have been collected in the Arabuko-Sokoke Forest) in coastal Kenya during August. Squeaks and squeaky trills, a "yi-yi-yi-yi-eek" were uttered by such small honeyguides interacting with Lesser Honeyguides (*I. minor*) and with Black-collared Barbets (*Lybius torquatus*). The trills are at a tempo of 11–12 per second, and notes have a terminal peak sonographically at about 2 kilohertz. Songlike "whee-ip" calls were heard from these small honeyguides in the dry forest canopy; the "whee-ip" notes were repeated at 1.3 per second. Structurally the notes have a double peak at 4–5 kilohertz, and they closely resemble such notes of *Indicator minor*, *I. conirostris*, and *I. exilis* (Chappuis, 1981), but they tend to be more clearly double peaked. Obviously the identity of the calling birds has to be corroborated to insure that these calls are indeed those of *I. narokensis* (see Short and Horne, 1979, sonograms of figs. 1 and 3).

VISUAL DISPLAYS: The crown feathers of birds suspected of representing this species were erected during interaction with barbets and with Lesser Honeyguides, and the black-tipped white outer tail feathers were spread in flight when these birds were chased by and otherwise interacted with barbets or honeyguides.

HOSTS: These are unknown. Individuals that called and were chased by Black-collared Barbets appeared to monitor pairs of the latter, and were driven from them by Lesser Honeyguides. The suggestion is that Black-collared Barbets may be one of its hosts.

TERRITORIALITY AND BREEDING BEHAVIOR: Information is lacking, except as noted above under Acoustic Displays and Hosts. Singing birds responded by approach to playback of



FIG. 4. First known photograph of *Indicator meliphilus* in front of experimental hive, November 1984.

their songs during August in coastal Kenya, and thus appeared to be territorial.

Indicator meliphilus (Oberholser)
Pallid Honeyguide (fig. 4)

RANGE SUMMARY: This small honeyguide occurs disjunctly in East Africa (eastern Uganda to central and southern Kenya and northern Tanzania), and from central Angola and southern Zaire through northern Zambia to Malawi, central Mozambique, and east-central Zimbabwe. Since it is easily confused with *Indicator narokensis* in East Africa, much care and collecting of specimens are required for identification, and field identification without the bird in hand is not feasible.

HABITAT: Occupies woodlands of diverse kinds including brachystegia woods, riverine woods in dry country, acacia woodland, fragmented forest patches, the edges of forests,

and, in Malawi, evergreen forest (Benson and Benson, 1977). The Pallid Honeyguide supposedly occurs in wetter habitats generally than does *I. narokensis*, but confusion of these two honeyguides makes it difficult to assess habitat preferences. Localities from which it is known range from sea level to about 2000 m (Britton, 1980).

FORAGING HABITS: These are mainly based upon reports of the southern population, which has fewer sympatric species with which it may be confused. Birds feed on wax from bees' nests, both occupied and unoccupied by the bees. Pallid Honeyguides creep about the bark of trees, going into cracks and holes. The birds are usually very active, in almost constant motion. Individuals glean in flowers and in the foliage, and flycatch for insects from a perch, often returning to the same perch (Carter, 1978). When seeking prey for flycatching, a honeyguide moves its head from side to side, peering, before darting after the insect (Carter, 1978). According to our Kenyan observations of a honeyguide likely to be of this species, the flycatching occurs both in low bushes and high in the canopy, and may take place over an extended period (15 minutes, one sortie per minute).

FOOD: It is known to eat beeswax, beetles, and otherwise undetermined insects. It feeds at flowers, most likely on insects taken from them. The regularity of its flycatching suggests that it feeds on various kinds of flying insects, and that insects form a significant portion of the diet. It does not guide to bees' nests, but feeds on beeswax obtained from active and abandoned hives that it finds.

INTERSPECIFIC BEHAVIOR: An individual apparently of this species, observed in central Kenya, was subordinate to *Indicator variiegatus* and *I. minor* at a source of beeswax, and its small size suggests that it regularly must give way to these and other larger honeyguides (among sympatric honeyguides only *I. narokensis* is smaller). In flycatching it frequently comes into conflict with other flycatching birds, and its aggressive manner of spreading its tail and swerving about brings it into encounters with other species. The Black-throated Wattle-Eye (*Platysteira peltata*), a flycatcher, has been noted attacking a Pallid Honeyguide (Carter, 1978). We have noted an individual likely to represent the

Pallid Honeyguide in flying attacks upon, and in chases involving, Black Tits (*Parus leucomelas*), warblers of the genus *Phylloscopus*, and Scimitarbills (*Phoeniculus cyanomelas*). During these pursuits the honeyguide exhibited great agility, speed, and maneuverability in evading and in circling its slower antagonists.

ACOUSTIC DISPLAYS: Its voice has not been recorded on tape. We have heard a suspected Pallid Honeyguide utter a short "dzzzz" trill during a chase involving a Scimitarbill, the trill resembling aggressive trills of *I. minor* and other honeyguides. We also heard a sharp "zit-zit" call from another (or the same) such bird a day later. Friedmann (1955, p. 226) noted a soft twittering sound of an apparent male near a suspected female, possibly a courtship call. Other notes ascribed to it are a rasping "zeet-zeet" in flight, a "zit-zit" as reported above (possibly the same call as the "zeet-zeet"), a chattering note, and a sibilant noise like whistling through one's teeth (see Friedmann, 1955). All of these and other calls require study and verification as to the species uttering them.

VISUAL DISPLAYS: The most conspicuous visual display is the frequent spreading or flicking of the tail, showing the white tips of the outer rectrices. This often is evident in Pallid Honeyguides giving chase to conspecific or other individuals, as well as in perched honeyguides. It seems to denote aggressiveness or assertiveness of the displaying honeyguide. A side-to-side movement of the head, as if to get a better view, is seen in perched Pallid Honeyguides, especially between bouts of flycatching—this could be a display, and certainly is a characteristic movement. Supposed courtship flight has been reported (Friedmann, 1955), one bird fanning the tail and flitting about another, uttering a twittering note (see Acoustic Displays), but, since the sexes cannot be distinguished, possibly this could represent an aggressive encounter between birds of the same sex.

HOSTS. These are unknown; hosts ascribed or reported are of doubtful validity. These are the Yellow-rumped Tinkerbird (*Pogonius bilineatus*, Friedmann, 1955, p. 227), Bennett's Woodpecker (*Campethera bennettii*, Benson and Benson, 1977, p. 114), and the Yellow-throated Petronia (*Petronia su-*

perciliarus, Mackworth-Praed and Grant 1970, p. 562).

TERRITORIALITY AND BREEDING HABITS: The only possible instance of territorial behavior has been mentioned above (see Visual Displays). Individuals are aggressive and likely to be territorial, for rarely are two individuals seen near one another, and they actively attack many small and even large birds of other species. Because of the uncertainty of the hosts, noted above, the breeding period is not well known, but it is likely to breed when small, hole-nesting hosts, perhaps tinkerbirds (*Pogoniulus* spp.), nest. Adults in breeding condition are reported from Tanzania in February (Brown and Britton, 1980), and Malawi in September. Immature specimens date from June and August in Kenya, from December in Tanzania, and from December and January in Zambia. Some of these data could conceivably represent *I. narokensis* rather than *I. meliphilus*.

Indicator exilis (Cassin)
Least Honeyguide

RANGE SUMMARY: The range of this forest species extends, perhaps disjunctly, from southern Senegal, Sierra Leone, and north-eastern Liberia (Colston, personal commun.) east to Ghana, and then from southwestern Nigeria east through southern Cameroun, southern Central African Republic, southern Sudan, Uganda, and western Kenya south to Bioko (Fernando Po), Gabon, Cabinda, northern Angola, northern Zambia, southern and eastern Zaire, and Burundi (Vande weghe, personal commun.). Adults are readily distinguished from other small honeyguides by the sharply contrasting blackish moustachial stripe and anterior forehead that set off the clear white loreal marks.

HABITAT: The Least Honeyguide basically is a forest-dwelling species, occurring as well in forest fringes, isolated forest patches, riverine forest, secondary forest, and trees in cultivated areas adjacent to forests. It extends from lowland forests near sea level to montane forest at elevations up to 2400 m in Kenya, Uganda, and eastern Zaire.

FORAGING HABITS: Most observations of this bird have been at bees' nests and honeycomb bait put out for collecting of specimens.

It also has been seen investigating tree cavities of diverse kinds, moving frequently at various levels in trees. As many as three birds have been observed near one another in the tops of trees. We have seen it flitting about the mid-level of a Kenyan forest canopy, gleaning in leaf clusters, flycatching sporadically, and moving frequently. Another bird moved along limbs and branches of forest trees, probing into mosses, lichens, and leaf petioles, and flycatching occasionally. Others have been noted flycatching and feeding by gleaning along the stem of a vertically hanging liana. Least Honeyguides are not known to guide humans or other mammals to beehives, and are presumed to find beeswax at occupied or unoccupied hives on their own.

FOODS: This honeyguide is known to eat beeswax, adult bees, bee grubs, hymenopterans of other kinds, aphids, ants, scale insects (possibly also their wax exudates), spiders, some fibers, possibly yellow pollen, seeds, and fruits (spp. undetermined).

INTERSPECIFIC BEHAVIOR: In Kakamega Forest, western Kenya we had *Indicator exilis* respond four times by close approach to the playback of the voices of the barbets *Tricholaema hirsuta* and (once) *Pogoniulus bilineatus*. In each case it perched nearby, flitted about spreading its tail, and looked at the recordist, over whom it circled (twice). Once it kept up its circling, with spread tail, fluttering. The honeyguide did not remain for more than a minute, after looking us over. It has been known to visit honeycomb sources used by *Indicator pumilio* (Chapin, 1958, 1962), and by *I. variegatus* (Archer and Glen, 1969), but relations between species at the hives or other sources have not been discussed.

ACOUSTIC DISPLAYS: Chappuis (1981) reported on the "song" of this honeyguide, a series very like that of the song of *I. minor*, but higher pitched and apparently lacking the initial, distinct note that characterizes the song of both *I. minor* and *I. conirostris*. This may be rendered "pew, pew, whew, whew, whew—" or a faster "wheer, wheer, wheer—" (from Chappuis' recordings, which we have heard and analyzed). The circumstances of the "song" utterances have not been described. In western Kenya we have heard a songlike "pee-pee-wheet, pee-pee-wheet" series, also

rendered "sweet-bee-bee." These "songs" were uttered by a lone bird perched at 10 m above a forest path in degraded forest during December 1983. Playback of the song or call resulted in close approach by the bird, that peered at us and looked from side to side, but did not call. We got no response from these Kenyan birds to playback of Chappuis' (1981) "songs" of *I. exilis* recorded in Cameroun.

The only other vocalizations reported are low siffling notes, and "tsa-tsa-tsa" calls, repeated in conflicts with one another, or in response to calls from other birds (Prigogine, 1971).

VISUAL DISPLAYS: Only a side-to-side movement of the head, by lone birds, and some erecting of crown feathers during playback response (presumably aggressive) are known visual displays.

HOSTS: The hosts invariably are stated to be tinkerbirds of diverse species (see, e.g., Friedmann, 1955). Bates (1930) reported young *I. exilis* found in the nests of unspecified barbets, and adults of this honeyguide entering holes excavated by the Yellow-rumped Tinkerbird (*Pogoniulus bilineatus*) and by the Gray-throated Barbet (*Gymnobucco bonapartei*)—the barbets were excited by the presence of this honeyguide. Nonetheless, there are no certain hosts as yet determined, and eggs reported are from the oviduct of adult females, not from hosts' nests. Reaction of adult Least Honeyguides to actual and played back vocalizations of the barbets *Pogoniulus bilineatus* and *Tricholaema hirsuta* suggests that these may be hosts.

TERRITORIALITY AND BREEDING HABITS: Aggressiveness of this honeyguide (Prigogine, 1971) suggests territoriality, but there are no details available on this aspect of its biology. There are no data on courtship. Breeding is indicated by a female held overnight on November 20, which laid an egg at Ilaro, Nigeria (Elgood, 1983), and by oviduct eggs ready to lay in June in north-central Zaire and in January in eastern Zaire. At Mt. Nimba, Liberia, an August adult female had laid, two females in November had large ovarian eggs, and a juvenile was taken in December (Colston, personal commun.). The duration of time over which the juvenal plumage is retained is unknown, but juvenal specimens are rep-

resented as follows: Bioko, June (also a June subadult, and May–June adults with enlarged gonads); Cameroun, April and June (plus May breeding noted); Congo, February; eastern Zaire, February, June (two), August, and October (three); and Sudan, February. Subadults and adults in breeding condition, taken with the juveniles just noted, suggest breeding from January to September in eastern Zaire, November to February in western Uganda, July to November in western Kenya, and September (perhaps earlier) to October in Zambia (data are from specimens and such sources as J. P. Chapin's carded notes, and Benson et al., 1971). Chapin's Tshibati, Zaire, specimens (Chapin 1958, 1962, specimens mainly in the AMNH) include fully juvenal-plumaged males with testes as large as 2 mm in diameter, and a subadult female having some juvenal feathers with an ovary as large as 4.5 by 3 mm. These data suggest that Little Honeyguides can breed before attaining a fully adult plumage (juvenal features include an essentially white tip on rectrices 3, 4, and 5, lack of a white loreal mark, the absence of a moustachial stripe, the lack of black on the forehead, and deeper gray-green underparts than in adults).

Indicator conirostris (Cassin)
Thick-billed Honeyguide

RANGE SUMMARY: This is a forest-inhabiting honeyguide that replaces its allospecies *I. minor* in the main forest region from Liberia, southern Ivory Coast, southern Ghana, and southern Nigeria east through central and southern Cameroun to southwestern Central African Republic, northern Zaire, western Uganda, and, disjunctly, western Kenya, south to northern Angola, and southern and eastern Zaire. It generally is considered uncommon. The status of this honeyguide with respect to *I. minor* needs clarification, as both occur together, or meet in some places in Uganda and western Kenya, but specimens intermediate between them are known for Nigeria, Cameroun, the Ruwenzori region of Zaire, and northern Angola. Both appear to have identical voices (Chappuis, 1981).

HABITAT: This forest honeyguide is replaced all about its range by *I. minor* in ad-

jacent woodland and semiopen country, although it does occur in dense second-growth in Liberia (specimen data), and in gallery forests of Angola and Nigeria (Elgood, 1983). It generally is a lowland forest species, but extends up to 2300 m in western Kenyan montane forests.

FORAGING HABITS: These are little known. Like all of its genus it frequents beehives, and it often is seen about the regularly active colonies of the barbets of the genus *Gymnobucco*. It flycatches for some insects, and comes to honeycomb put out as bait. This honeyguide is not known to guide humans or other mammals to honey sources.

FOODS: It eats beeswax, bees, beetles, flying termites, and other insects. The remains of figs, other fruit, black seeds, and plant fibers have been noted in stomachs of adults. That some fruit is taken is not surprising, for barbets and other hosts regularly feed fruit to nestling honeyguides, which obviously fledge successfully on a diet including much fruit.

INTERSPECIFIC BEHAVIOR: No information is available about this honeyguide and its relations with host species, or, especially, with the broadly sympatric and morphologically very similar, though smaller, *Indicator exilis*.

ACOUSTIC DISPLAYS: Its song is so like that of *I. minor* as to be indistinguishable. Tape recordings of its song lent us for analysis by C. Chappuis suggest that it possibly sings slightly faster (but this may be insignificant, given variation in songs of *I. minor*), but in pitch, quality, and structure its notes are like those of *I. minor* (see Chappuis, 1981), that is, an introductory, dropping "wheew" followed at 0.8 to 1.0 second intervals by four to seven, double-peaked, sharp "wheet" notes. Most field workers consider this a quiet species, and it is noteworthy that such a careful observer as Chapin never heard its voice in all his time spent in the Congo region. Literature references give only a chirping call for it, but it is likely to utter squeaking and trilling calls similar to those known for *I. minor*.

VISUAL DISPLAYS: Unknown.

HOSTS: The only definitely ascribed host is the Gray-throated Barbet (*Gymnobucco bonapartei*), but it frequents colonies of Naked-faced Barbets (*G. calvus*) throughout the year and hence it very likely uses that barbet (and



FIG. 5. Lesser Honeyguide (*Indicator minor*) just below experimental hive.

most likely the other two species of *Gymnobucco* as well) as a major host (Friedmann, 1955). The only other species suggested as a host is the tinkerbird, *Pogoniulus bilineatus*, for which the single record is doubtful (Friedmann, 1955).

TERRITORIALITY AND BREEDING HABITS: There are no data concerning territorial behavior, or breeding habits other than records from collected specimens (in addition to observations of Thick-billed Honeyguides regularly seen in the vicinity of nests of the social barbets of the genus *Gymnobucco*). Adult females with large eggs are known from Liberia in September (egg in oviduct), and from eastern Zaire in December, and an egg was reported from Cameroun in October. Large gonads mark adults from: Liberia in November; Ghana in February; Nigeria in May, August, October, and December; Uganda and Kenya in December; Zaire in October to December; and Angola in February. Juveniles were found in April from Cameroun and June (nestling) from western Kenya, and an April Cameroun specimen is subadult.

Indicator minor Stephens
Lesser Honeyguide (figs. 5, 7, 8)

RANGE SUMMARY: Generally this common honeyguide occurs around the Afrotropical

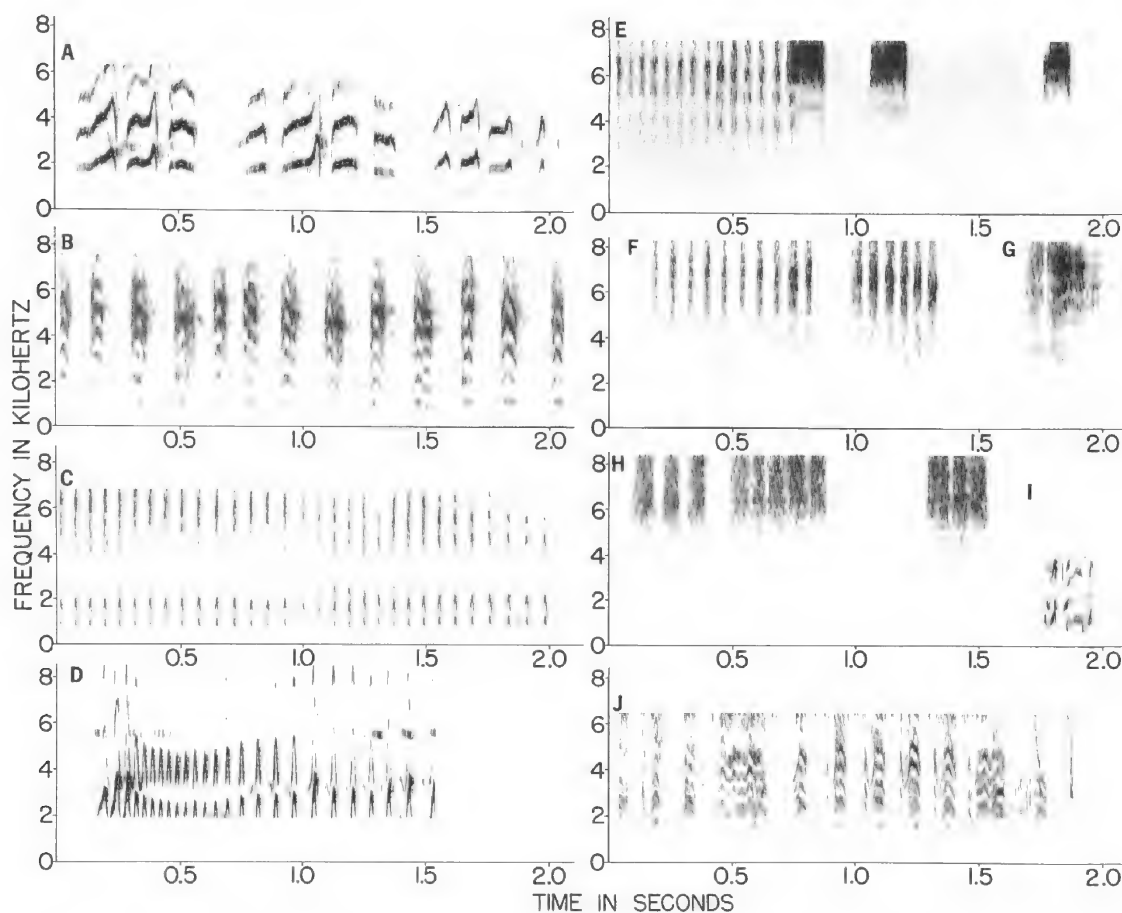


FIG. 6. Vocalizations of Lesser, Scaly-throated, and Greater honeyguides, all in wide-band sonagrams. A. Three variant songs of a single male Lesser Honeyguide (collected specimen), rendered, from left to right "pwee-weet-wee," "pwa-weet-wee-waa," and "wee-tya-wee-wit," Nov. 19, 1981, Arabuko-Sokoke Forest, coastal Kenya. B. Notes 8 to 20 of a 32-note squeaky trill ("tyeep" notes) of Lesser Honeyguide directed at White-headed Barbet (*Lybius leucocephalus*), September 1979, Karen, Kenya. C. Slightly wavering aggressive trill during interactions of two Lesser Honeyguides, Nov. 21, 1981, Arabuko-Sokoke Forest, coastal Kenya. D. Wavering aggressive trill of Lesser Honeyguide, Jan. 6, 1982, Akagera Park, Rwanda (disregard barlike elements at start and finish at about 5.5 kilohertz). E. Calls of two Scaly-throated Honeyguides in aggressive encounter over experimental honeycomb site, one giving chattery trill, other uttering screechy, long notes, Dec. 19, 1983, Ol Ari Nyiro, central Kenya. F. Two noisy chattery bursts of interacting Scaly-throated Honeyguides over honeycomb, Dec. 17, 1983, Ol Ari Nyiro, Kenya. G. Long screechy burst, interacting Scaly-throated Honeyguides, Dec. 17, 1983, Ol Ari Nyiro, Kenya. H. Hissing chattery birds, notes longer than in chattery trills but shorter than screechy notes (see E, F, G), of Scaly-throated Honeyguide in an encounter with another conspecific bird, Dec. 19, 1983, Ol Ari Nyiro, Kenya. I. "Tya-dah," double-noted call of interacting Scaly-throated Honeyguides, Dec. 17, 1983, Ol Ari Nyiro, Kenya. J. Long series of squeaky calls by male Greater Honeyguide in close pursuit of an African Drongo (*Dicrurus adsimilis*), Nov. 22, 1981, Arabuko-Sokoke Forest, coastal Kenya.

belt from Senegal, Mali, Chad, southern and eastern Sudan, northern Ethiopia and northern Somalia south in unforested areas to southern Guinea, northern Ivory Coast, central Ghana, Nigeria, central Cameroun,

southern Central African Republic, northeastern and eastern Zaire, Burundi, and Tanzania; and, south of the forest from northern Angola, southern Zaire, Burundi, and Tanzania south to southern Angola, northern Na-



FIG. 7. Nestling Lesser Honeyguide being fed (fruit) by adult Anchieta's Barbet (*Stactolaema anchietae*) for the last time before it departed the nest, not five minutes later. Near Ndola, Zambia, November 1983.

mibia, northern and eastern Botswana, Orange Free State, southwestern Cape Province, Lesotho, Natal, Swaziland, and southern Mozambique, except in treeless areas. It apparently interbreeds with *I. conirostris* in Nigeria and Cameroun (personal observ.), and perhaps in Angola, but is usually ecologically separated from that forest-dwelling species, which it meets parapatrically in Sudan, Kenya, and Uganda.

HABITAT: It occupies woodlands, wooded grassland, brushland, and the edges of forests, as well as cultivated areas with trees, avoiding the interior of forests, and treeless grasslands and deserts. A broad range of elevations from sea level to 3000 m (East Africa) is occupied (Britton, 1980), although it usually occurs below 2000 m.

FORAGING HABITS: This honeyguide is adroit at flycatching for insects, and it also gleans on the bark and in the foliage of trees. It seeks beeswax from occupied and aban-



FIG. 8. Nestling Lesser Honeyguide of figure 7 just about to leave foster parent Anchieta's Barbet nest, same date and locality.

doned beehives, without guiding mammals to them, regularly investigating crevices, holes in trees, and recently opened (by humans) hives. Usually solitary, two may occur near a beehive, and it sometimes is seen in the company of *Indicator indicator* or *I. variegatus* at hives. At times it flies to isolated trees in cultivated areas where it may sing or forage. We have observed Lesser Honeyguides probing and gleaning on the bark of rough-barked trees in a woodpecker-like manner. When perched, it often crouches, as if seeking prey, at which times the small-headedness of the species is most evident. Between foraging sites it often flies in a dipping pattern and flicks its white-tipped tail periodically; it may fly directly, as well, without undulations, or pause to chase individuals of other species that it may encounter. Water sources, such as small streams or bird watering baths put out by humans, are visited, and the bird drinks water occasionally.

FOODS: The Lesser Honeyguide regularly seeks out and eats beeswax, apparently digesting it by the action of aerobic lipolytic bacteria (Friedmann and Kern, 1956), although A. W. Diamond (*in litt.*) and others question the efficacy of aerobic bacterial digestion in the relatively anaerobic gut. When

offered a choice of plain beeswax or brown, honeyed wax containing bits of bees and honey, they consistently choose the plain wax. They also eat adult bees at hives, and "hawk" or flycatch for mayflies, winged termites, ants, hymenopterous insects other than bees (e.g., larvae and pupae of aculeate wasps), caterpillars, and spiders (Friedmann, 1955; personal observ.). Undetermined plant remains, seeds, and hairlike threads are known from stomachs of collected honeyguides. This species may kill and eat small birds on rare occasions (Friedmann, 1955). Young are fed many kinds of insects, and berries and other fruits by their foster parents (often barbets and woodpeckers).

INTERSPECIFIC BEHAVIOR: Other than many honeyguide-host interactions, reported below, this fast and aggressive honeyguide frequently engages in encounters with various, usually small, birds such as bulbuls (*Pycnonotus* spp.), Fiscal Shrikes (*Lanius collaris*), flycatchers (e.g., *Batis molitor*), and many others (Friedmann, 1955; Ranger, 1955; personal observ.). The honeyguide may initiate these without provocation, but its flitting and tail-spreading while making sallies for insects sometimes trigger an attack by another species—the honeyguide quickly becomes the aggressor unless the interactive species is very much larger. This honeyguide regularly attacks and drives away smaller honeyguides, e.g., *Indicator narokensis* and *I. meliphilus* that it chances to find, and is dominant to them at beeswax sources. Its activities bring it into conflict with the considerably larger *Indicator indicator* and *I. variegatus*, especially near wax sources. These larger honeyguides are dominant over *I. minor*, and may chase the latter. However, *I. minor* is faster and more agile than are *variegatus* and *indicator*, and it may briefly return the attack, or, more frequently, it evades the slower attacker and circles back to the wax source. In this manner it is able to dart in, and secure a few pieces of wax before the larger honeyguide returns and supplants it (personal observ.). We have seen it attack Tree Pipits (*Anthus trivialis*), which have white tips of the outer tail like honeyguides, as the latter birds fly up to a tree after feeding on the ground.

ACOUSTIC DISPLAYS: Nestling Lesser Honeyguides utter squeaky notes in long series

that function sufficiently as begging calls to cause feeding by the foster parents. Adults make ruffling, mechanical sounds with the wings as they interact with one another or with other species. Other mechanical sounds include a so-called drumming flight display made as one or two birds fly in bounding flights up and down, with circling, fluttering, and gliding movements. This sound is made by the tail (Friedmann, 1955), which often is spread during the flight display. The "drumming" has been compared with the sound of an irregularly firing motorcycle motor by Brown (1948). Near beehives a clicklike note has been heard, and a strident alarm call, a "kish-kish-kish-," is known (Friedmann, 1955). Squeaks, squeak-trills (fig. 6B), and trill-squeaks are uttered singly or in series, speeding to a rattling "tyeek-tyik-tyik-tyik-ik-ik-ikikik" (Short and Horne, 1979), marking interactions of Lesser Honeyguides intraspecifically and interspecifically. These may range from very squeaky and slow, at five notes per second, to a fast, sharp "ddddd" at up to 30 notes per second continued for 2 to 3 seconds. The call may waver in pitch between 1.3 and 2.7 kilohertz, and often slows in tempo toward the end. More squeaklike trills are softer, and probably function at close range in encounters, whereas louder trills (fig. 6C, D) are characteristic of chases, and of long-range interactions between honeyguides, or between honeyguides and barbets (or woodpeckers). Actual contact and battles often are marked by fast, high-pitched trills (personal observ.). These trills are commonly heard during the breeding season of this honeyguide's hosts.

In a letter of July 25, 1948, to J. P. Chapin, Captain C. R. S. Pitman (unpublished files of Dr. Chapin) reported a "pee-euw, pee-euw, pee-euw" given during the dipping portions of the flight of two possibly paired birds as they moved from tree to tree. This call closely resembles the so-called song (Friedmann, 1955), a series of ten to 30 "weet," "pew," or "wit" notes, introduced by a distinctive, single "pee-yew" or "whee-ew" that may not be audible to an observer at a distance from the honeyguide (Short and Horne, unpublished analyses). The main series of "pew" notes carries farther, to 365 m (Ranger, 1955). Heard so far only from males, this repetitive

series of notes at about two per second is delivered for periods of a few minutes to two hours or more at 0.5 to 3.0 series per minute. It characteristically is given from a regularly used site, usually beneath the canopy of a tree. In our experience the sites are not so specific as indicated by Friedmann (1955). Rather, they are areas within a tree or even a tree itself, and not a specific branch (one bird in western Kenya sang from at least six points on all sides of a single tree). So-called song perches, which may be taken to mean a general site (e.g., a particular tree), appear to be traditional, and are used for long periods of the year in southern Africa (see under Territoriality and Breeding Habits). In eastern Africa the song occurs over a shorter period, and indeed may be replaced by other calls that we have heard as far south as Zambia (personal observ., see below).

The introductory "pee-yew" note of the typical song drops from an early peak of about 4, to as low as 2 kilohertz, often with a step, and it lasts about 0.2 second. "Pew" notes of the song are shorter, at 0.1 second, and they vary from being double-peaked to single-peaked at about 4 kilohertz. These notes are extremely similar to, if not identical with, the song notes of *I. conirostris* (Chappuis, 1981). Overtones are marked in both the "pee-yew" and "pew" notes.

Loud, clear songlike notes in series are more frequent in Kenya than are the songs described above. These repeated series vary in form and length, from a short "pwee-wit," to phrases such as "pwee-wit-weet" and "pwee-weet-tya-ya-ya-ya." Some variants are shown in figure 6A. Sharper notes among these tend to resemble the double, introductory note of the song, described above, but they terminate, rather than begin with, a peak at 2.5 to 3 kilohertz. Strong overtones occur in this song form, which varies in duration from 0.5 second for a three-noted version to 1.2 second for those of seven or eight notes. Such "songs" also have been recorded by us on tape in Zambia, as for example, a "wa-weet-weep-weet" from a Lesser Honeyguide in November 1983 (near Ndola, northern Zambia). The relation of this song form to the typical song described above remains to be elucidated. We note that the variant "songs" are even less often delivered from

special song perches than are the typical songs. These short variant songs often are uttered in the vicinity of singing (duetting) pairs or groups of the barbet hosts of this honeyguide, e.g., *Lybius leucocephalus* and *L. torquatus* (Short and Horne, 1979) in Kenya, and *Stactolaema anchietae* and *Lybius chaplini* in Zambia (personal observ.). Lesser Honeyguides regularly come to our playback of the songs and duets of these and other barbets; the barbets likewise approach and act aggressively (calls, displays) when we play back Lesser Honeyguide trill calls.

VISUAL DISPLAYS: Tail spreading is an aggressive and assertive display given in flight, when one bird pursues another or sometimes when no antagonist is apparent, and also while a bird is perched and interacting with other birds. When aggressively trilling, as in response to playback and approach to the recordist, the bird often flicks the wings and moves the head from side-to-side as if peering to detect another bird. At such times the bird often hunches its back, head lowered. Since the spread tail is so conspicuous, the Lesser Honeyguide seems to control its spread very finely; when sneaking about near a host's nest, or when moving to a beeswax source in the presence of larger species of honeyguides, the white of the outer tail is completely hidden from view dorsally, being covered by the greenish central tail feathers.

During encounters with hosts such as barbets, the Lesser Honeyguide may spread its tail and half-glide into a perch, or give a peculiar fluttering, then sail to a perch. These call attention to the often-calling honeyguide, and could serve to attract barbets from the nest area to attack the honeyguide. Since a second honeyguide sometimes is present, perched unobtrusively (and often passing undetected by human observers), these flight displays may be intraspecifically aggressive, or even sexual in connotation, but such functions require further study for elucidation. Other flight displays that involve "drumming" sounds made with the tail possibly are territorial (Ranger, 1955). Two Lesser Honeyguides may fly together in dipping flight that has been taken to reflect courtship (Friedmann, 1955).

Gaping is performed by Lesser Honeyguides that are attacked by other conspecific

birds. During encounters, the bird attacked seems to maintain a sleeked plumage, whereas the attacker often has the feathers of the head, back, and thighs erected.

Special mention should be made of the flight of this honeyguide, as it probably conveys certain meaning to the birds beyond the display flights noted above. Lesser Honeyguides can fly directly, or dip and undulate in flight. They are extremely fast and maneuverable, completely outclassing their host woodpeckers, and generally barbets as well (only *Stactolaema whytii* and *S. anchietae*, of all the barbets we have observed interacting with Lesser Honeyguides, can catch them in flight with any regularity). When interacting closely in chases, Lesser Honeyguides make rustling sounds with the wings, flailing with them. Many times we have seen a barbet chase a Lesser Honeyguide from one tree, only to have the honeyguide chasing it, pecking it, and beating it with its wings before the two reach an adjacent tree, where the barbet usually lands. It is clear to us that Lesser Honeyguides indeed entice barbets to chase them, usually resulting in rapid tiring of the barbets, doubtless to the honeyguide's advantage (see below).

HOSTS: The hosts of this honeyguide all are hole-nesters, chiefly barbets and woodpeckers, but with two each of bee-eaters and starlings, and several of other groups. We consider the following to be sufficiently documented to be accepted (Friedmann, 1955). The bee-eaters are *Merops pusillus* and *M. oreobates* (Friedmann, 1958). The barbets are: *Stactolaema whytii*, *S. anchietae* (Zambia, 1983, personal observ. of fledging Lesser Honeyguide), *S. olivacea*, *Tricholaema leucomelaina*, *T. diademata*, *Lybius chaplini* (Colebrook-Robjent and Stjernstedt, 1976), *L. leucocephalus* (Friedmann, 1970; Short and Horne, 1979), *L. torquatus* and *Trachyphonus vaillantii*. Woodpeckers parasitized include: *Jynx ruficollis*, *Campethera bennettii*, and *C. abingoni*. The starlings are *Spreo bicolor* and *Cinnyricinclus leucogaster*. The other hosts are: Striped Kingfisher (*Halcyon chelicuti*), White-throated Swallow (*Hirundo albigularis*), and Yellow-throated Petronia (*Petronia superciliaris*).

The information available to us suggests these likely hosts, for which conclusive evi-

dence is as yet unavailable: the barbets *Stactolaema leucotis* (personal observ.) and *Lybius vieilloti*, and the Cardinal Woodpecker (*Dendropicos fuscescens*). Possible hosts for which data so far are inconclusive, or reports which require confirmation are: Red-fronted Tinkerbird (*Pogoniulus pusillus*), Yellow-fronted Tinkerbird (*P. chrysoconus*), Gray-throated Barbet (Lesser Honeyguides about active nests, personal observ.), Olive Woodpecker (*Dendropicos griseocephalus*), Gray Woodpecker (*D. goertae*), Greater Striped Swallow (*Hirundo cucullata*), Gray Tit (*Parus afer*), and Southern Black Tit (*P. niger*, the species of *Indicator* is uncertain, Friedmann, 1955).

Many of the species known to be hosts have close relatives elsewhere within the range of *I. minor*, and at least some of these (e.g., *Lybius guifsobalito*, *L. rubrifacies*, *Tricholaema frontata*) should prove to be hosts of this honeyguide.

Lists of hosts in themselves are apt to be deceptive. It is clear that barbets generally are the preferred hosts of the Lesser Honeyguide, and that locally, one barbet species may be preferred. Of 33 cases of hosts from Zimbabwe (Stuart Irwin, 1981), 23 are of barbets and 20 of these are of *Lybius torquatus* (but nine are of the bee-eater *Merops pusillus*). Likewise, most records from Zaire (35 of 50) represent barbet hosts.

TERRITORIALITY AND BREEDING HABITS: Pair relations and the occurrence of territoriality are under study. It is clear that the Lesser Honeyguide's breeding is more complicated than it appeared to be earlier (Friedmann, 1955). It is the usual conception that males in the breeding season sing from specific calling sites that are not defended, but may be used alternately by two or more males (rarely two sing simultaneously from the same site, Ranger, 1955), and that females come to these sites to select a mate. In fact we can find no report of copulation at the calling sites, or "stud posts" (Friedmann, 1955) as they are designated, and we have noted (personal observ.) signs of aggression between honeyguides at diverse times of the year. Calling sites that we have observed in Kenya are no more specific than the top of a particular tree, and the presumed males that sing at them are highly aggressive to other singing

Lesser Honeyguides that intrude, and to (human) playback of these songs.

In southern Africa north to southern Zaire, songs are uttered from the calling sites for six to eight months of the year, generally in August to March. In central and eastern Kenya we have rarely heard singing birds despite field studies covering diverse seasons in the years 1976 to 1984. Secondary songs (see above) were heard more frequently in Kenya.

Lesser Honeyguides regularly investigate used and vacant holes in trees (personal observ.), and they monitor and defend (probably only the males) duetting barbet pairs from other conspecific individuals, even when the barbets are not nesting (e.g., *Lybius torquatus*, Short and Horne, 1983; see also Short and Horne, 1979). As many as four males replaced one another when collected in the company of, and defending, a duetting barbet pair (Short and Horne, 1983). Lesser Honeyguides have been seen by us at the roosting holes of nonbreeding groups of *Stactolaema whytii*, *Lybius melanopterus*, *L. torquatus*, and *Gymnobucco bonapartei*, in most cases resulting in attacks and supplanting by the barbets (personal observ.).

In one Zambian case a Lesser Honeyguide (there may have been more than one) consistently approached the nest of a group of Anchieta's Barbets (*Stactolaema*) that contained only a young Lesser Honeyguide, with daily visits involving calls and encounters between the adult honeyguide and the barbets. A Lesser Honeyguide visited the nest, calling, and was seen by (and saw) the young honeyguide moments before the latter fledged. The baby honeyguide had been fed regularly by its foster parents (figs. 7, 8) and at least two other adult members of the group, with all of which it roosted nightly in the nest. Immediately on its flying from the nest for the first and only time, an approaching Anchieta's Barbet carrying food to feed the young honeyguide shifted from a "parental" to a defensive role, attacking the youngster repeatedly. Two adult barbets pursued the honeyguide, hitting it in flight and chasing it beyond the limits of the barbets' territory. (It is noteworthy that the characteristic honeyguide tail pattern could not be seen *inside* the nest, but became apparent instantly as the bird flew, this seeming to trigger the change

in the barbets' behavior.) There followed repeated visits to the empty nest by at least two adult barbets carrying food (whether these included those that chased the honeyguide is uncertain), apparently bewildered by the sudden disappearance of "their" young—they carried fruit to the nest, about it, into it, and out, several times. Within 15 minutes an *adult* Lesser Honeyguide appeared, or reappeared, approaching the nest and looking inside, despite attacks and pursuits by one or another of the Anchieta's Barbets. The honeyguide also peered into an older excavated hole located above the actual nest (all from field notes and personal observations near Ndola, Zambia, in November 1983).

During nesting of the barbets, Lesser Honeyguides frequently are in attendance, although they may be inconspicuous except when trying to look into, or enter, the nest. On more than 40 occasions (of more than 500) in which we observed interactions of a Lesser Honeyguide with individuals of various species of barbet near a nest, we have at least glimpsed a second, silent, apparently secretive Lesser Honeyguide nearby. These figures are conservative, and are inexact because we generally assumed that when one or two barbets left chasing a honeyguide, and later returned with a honeyguide accompanying them, the *same* Lesser Honeyguide was involved. Since the birds at times were away for one-half hour or more, and we often saw a honeyguide while hearing a continuing chase of barbets and honeyguides in the distance, more cases are likely in both categories. In addition, there are 55 cases in which a second Lesser Honeyguide appeared and then called, and became involved aggressively with the honeyguide already present (these likely represent male-male encounters). Since Lesser Honeyguides perch frequently in the foliage, and when quiet are very difficult to locate, it is likely that a second honeyguide was present more often than is indicated by our observations.

Post-breeding Nubian Woodpeckers (*Campethera nubica*) and Bennett's Woodpeckers (*C. bennettii*) also have been observed being followed, approached closely, and attacked by attendant Lesser Honeyguides. The woodpeckers are less able than barbets to chase the honeyguides away, and

to pursue them with any ease, because they are too slow and heavy. They engaged in long (to 40 minutes) engagements with Lesser Honeyguides, undoubtedly to the detriment of the woodpeckers' own accompanying young (in the case of the Nubian Woodpeckers).

Another incident shedding light upon the relation of the Lesser Honeyguide's behavior to activities of its hosts occurred in November 1983, north of Choma, Zambia. A group of Chaplin's Barbets (*Lybius chaplini*) attended a nest. There were occasional duets of two and even three of the four or five adults in the group. One and at times two Lesser Honeyguides were active about the nest, chasing individual barbets, enticing them to attack, and breaking up duets. Following one of these broken duets and a subsequent chase of a honeyguide by one barbet, the barbet in the nest suddenly appeared at the entrance with an egg in its bill. It left the nest, perched nearby, and crushed and dropped the egg. To our surprise, the same barbet returned to the nest, entered, came out with a second egg that it then broke, and methodically repeated this twice more, breaking four eggs in all. We later recovered the completely smashed, fresh eggs (hardly, if at all, incubated), and studied them with Mr. Colebrook-Robjent, a veteran egg collector who had first described the eggs of this barbet (Colebrook-Robjent and Stjernstedt, 1976). He stated that each was clearly a barbet egg, and *not* a honeyguide egg. We have no reason to doubt this.

What can we conclude from these observations? Obviously the matters of Lesser Honeyguide territoriality and relations with their hosts require additional study. It seems evident that the situation is complicated (it may be that there is geographic variation in these details). The available data show that the Lesser Honeyguides, at least in some cases, carefully and frequently monitor the activities of their hosts. They also react to the duets or playbacks of the duets of their hosts even when the latter are not breeding, inciting aggression, fighting among themselves, and closely following the hosts about (Short and Horne, 1983). They seem particularly interested in holes used by the hosts for roosting and nesting, and frequently fly to these to examine them when not under observation

by the host species. The facts of the close monitoring of hosts' holes and nests, even when the latter already have a young Lesser Honeyguide inside, frequent conflicts between male honeyguides (Short and Horne, 1983) in proximity to the hosts, and the honeyguide-related destruction of barbet eggs by barbets suggest that hosts' holes and activities are related to territoriality, of some form, in the Lesser Honeyguide, and that the honeyguide can influence hosts' nesting whether already parasitized or not. It is clear that hosts' activities attract honeyguides, and the duets and other actions of hosts can serve as clues to direct the attention of male and female Lesser Honeyguides not only to the host, but to the resident Lesser Honeyguide as well. Limited data even suggest that young honeyguides in the nests of foster parents may be visited by adult honeyguides, and thus exposed to the appearance and calls of conspecific adults. Finally, our data suggest frequent action in concert at prospective host nests by two Lesser Honeyguides, presumably paired birds, for male Lesser Honeyguides instantly cease activities with hosts to attack some incoming honeyguides (males, as shown in Short and Horne, 1983), but move freely about with the hosts while ignoring, or even perching with, some other conspecific birds (likely females, see Short and Horne, 1979, pp. 9, 11). Associations of male and female Lesser Honeyguides were reported by Roberts (1956). Hoesch (1957) noted two cases of apparent pairs, or in any case two, Lesser Honeyguides supposedly assisting pairs of the barbet *Tricholaema leucomelaina* (a host) to drive away the barbet's nest-hole competitors, Rüppell's Parrots (*Poicephalus rueppellii*).

Female Lesser Honeyguides are reported (Friedmann, 1955) to occasionally remove the eggs of the hosts in whose nest they lay, but it is likely that the hatchling Lesser Honeyguide, with its sharply hooked bill, is mainly responsible for killing the hosts' young, or destroying their eggs. The dead young are removed from the nest by the foster parents (Friedmann, 1955). We have found no records of two Lesser Honeyguides being raised simultaneously by any of its hosts. Attempts by adult Lesser Honeyguides to enter occupied barbet nests are resisted vigorously, and Moyer's report (1980) of a Lesser Honey-

guide caught in the nest of, and apparently killed by Black-collared Barbets (*Lybius torquatus*) indicates the risks that are taken by the honeyguides.

There are no data on laying schedules of females, or on whether a single female utilizes several host species, or specializes on one alone. Sparse data suggest that individual Lesser Honeyguides, probably males, at least are attracted by calls and activities of two (or more) host species, e.g., Anchieta's Barbet and Black-collared Barbet in Zambia (personal observ.).

The breeding period of this honeyguide is diverse, as its wide distribution and many hosts suggest. Brown and Britton (1980, p. 75) give about ten East African breeding records in the period April to August, during and just after the main rains. Many host barbets in that region nest in the dry season (personal observ.), so we consider the few records of Brown and Britton insufficient to establish a pattern. Specimen records include two females with a shelled egg in the oviduct from Kenya in January, and one from northeastern Tanzania in February, outside of the months they report; juveniles from Kenya date April to December. Other laying dates are September to November in Zambia (Benson et al., 1971; person. observ.) and Malawi (Benson and Benson, 1977), September to January in Zimbabwe (Stuart Irwin, 1981; 30 of 35 records date October and November), and, from various sources, September to February (mainly October to December) in South Africa. Juveniles from Uganda date November and December, and from eastern Zaire in October. Breeding is reported, with bases not always certain, or adults with enlarged gonads are noted (see Friedmann, 1955) from Senegal and Gambia in May and June, Sudan in March, southern Somalia in March, Uganda in October to December, southern Zaire in September to December, Angola in November, and northern Botswana in November.

The Lesser Honeyguide's incubation period of 12 to an estimated 16 and one-half days (three records, Friedmann, 1955) is less than that of hosts, whereas the nestling period in two cases was 38 days, longer than that of the host Black-collared Barbets. (The long nestling period suggests that the young hon-

eyguide must be able to fend for itself, mainly or entirely, on fledging, as Ranger, 1955, p. 86, also suggested.) The young are fed on the foods of the hosts, which often include fruits, and, of course, do not include wax.

The young are born naked, with a bill hook that is shed in 12 to 15 days (Ranger, 1955). They kill their host's young within the first week, generally, and attempt to bite humans when handled for two weeks after hatching, but not thereafter (Ranger, 1955). No host's young are known to have survived with a young Lesser Honeyguide, which, when barbets are the host, thus has to itself all of the food brought by its foster parents and the helpers usually found in various species of barbets. The feathers of the naked hatchling emerge in 7 to 12 days, and the eyes open in 11 to 20 days (Ranger, 1955). Most Lesser Honeyguides hosted by barbets probably leave the foster parents, at the latter's urging, when they fledge. The young honeyguide in any case does not return to the nesting cavity (as do the host's young), thus resulting in a situation unusual for the foster parents of whatever host species. Reports of foster parents feeding the young Lesser Honeyguide are based upon circumstantial and unconvincing evidence (see Friedmann, 1955, pp. 210, 212), and we frankly doubt that the hosts continue feeding the newly fledged Lesser Honeyguide.

Indicator maculatus G. R. Gray
Spotted Honeyguide

RANGE SUMMARY: This honeyguide occupies a range complementing that of its allo-species, *I. variegatus*, in forests from Gambia and Guinea-Bissau across West Africa through all of Sierra Leone, and through Ivory coast and Ghana to southern Nigeria, then eastward through southern Cameroun, northern Zaire, the Ouossi River region of southeastern Central African Republic, southern Sudan, and southwestern Uganda, and southward to Gabon, Cabinda, and central and eastern Zaire. It is narrowly sympatric with *I. variegatus* in southern Sudan (Nikolaus, 1982) and western Uganda (Friedmann and Williams, 1971).

HABITAT: It occupies forests, forest clearings and edges, gallery forests, and dense thickets that are in proximity to forests. It

ranges from sea level to 1650 m in Cameroun (specimens) mountains, to 1500 m in eastern Zaire, and reaches a maximum elevation of 2100 m in southern Sudan (Nikolaus, 1982).

FORAGING HABITS: It is suggested (Friedmann, 1955) that the Spotted Honeyguide forages in a manner similar to that of its close relative, *I. variegatus*. It seeks beeswax, which it eats, and it readily comes to beeswax placed out for it by humans (Friedmann, 1978a). The diet from stomach contents suggests that it flycatches for insects and takes these and spiders from the bark and foliage of trees.

FOODS: Stomach contents include spiders of diverse sizes, as well as caterpillars, beetles, ants, and termites. Beeswax frequently is found, as well as small seeds, probably from fruits, pollen, and sand grains.

INTERSPECIFIC BEHAVIOR: There are no data.

ACOUSTIC DISPLAYS: Its voice has not been tape recorded. Nikolaus (1982, p. 3) described a loud call, probably that noted in most of the literature (see Friedmann, 1955) as "woe-woe-woe-," as follows: "like that of a small falcon or similar to the call of the Long-crested Eagle *Lophoaeetus occipitalis*, but a little higher pitched." Many authors report that it has a trill or purring call very like the main trilling call or song (delivered from "specific" song perches) of the Scaly-throated Honeyguide, whose song bears resemblance to the songs of the barbets *Lybius bidentatus* and *Trachyphonus vaillantii* (personal observ.).

VISUAL DISPLAYS: These probably are like those of *I. variegatus*. Its trilling song is delivered with throat and body feathers erected.

HOSTS: These are as yet unknown. The presumption is that the Gray-throated Barbet (*Gymnobucco bonapartei*) and others of the genus *Gymnobucco* are hosts (Friedmann, 1955). The very striking resemblance in detail of the head, throat, and breast patterns and colors of *I. maculatus* to those of the Buff-spotted Woodpecker (*Campethera nivosus*) suggest that this may be a major host, but supportive data are lacking. Its range generally correlates with that of this woodpecker.

TERRITORIALITY AND BREEDING HABITS: As its hosts are uncertain, there is little breeding information and there are no data on territoriality. Eggs are known from two females that dropped them, one each, in mist nets in

which the birds had been trapped. These eggs date January in Rio Muni (Friedmann, 1955), representing *Indicator maculatus stictothorax*, and June from Ivory Coast (Friedmann, 1970), representing *I. m. maculatus*. Juveniles, which have a distinctive breast pattern and whiter tail tips than do adults, are known from the Ivory Coast in June, Cameroun and Gabon in August, and Sudan in March. Adults with gonads that are enlarged, and thus may be in or near breeding condition, represent Sierra Leone in March, Central African Republic in May and June (Friedmann, 1978a), Sudan in March (Traylor and Archer, 1982), and Uganda in July. There are reports of breeding from Cameroun in November, northern Zaire in November to March, and eastern Zaire in February to March (Friedmann, 1955). Molting birds represent the areas and months of the year indicated by laying dates and juveniles, and, in general, honeyguides seem to molt from the main part of the breeding season until just thereafter (personal observ.).

Indicator variegatus Lesson
Scaly-throated (or Variegated)
Honeyguide (figs. 9-18)

RANGE SUMMARY: This honeyguide occupies a parapatric range east and south of that of its close relative, *I. maculatus*, with which it forms a superspecies (the two meet at least in southern Sudan, and Bwamba Forest, southwestern Uganda, and probably in northeastern Zaire, see *I. maculatus*). The range of *variegatus* extends from southern Sudan, most of Uganda, central Ethiopia, and southern Somalia south (with gaps in arid areas lacking dense brush) around the eastern fringe of Zaire and through Zambia west to north-central Angola, then south to southwestern Angola, northeastern Zimbabwe, Swaziland, eastern Transvaal, Natal, and to coastal eastern Cape Province in South Africa, and to Mozambique in the east.

HABITAT: The Scaly-throated Honeyguide is a generally inconspicuous and even secretive resident of thickets, woodlands, riverine forests, and forest edges and clearings. In dry bushland areas it is restricted to thickets and streamside denser brush. Where its range approaches that of allospecies *I. maculatus* in



FIG. 9. Adult Scaly-throated Honeyguide (*Indicator variegatus*) below the experimental hive of figure 3. Posture typical.

easternmost Zaire it avoids forest and is found in wooded grasslands and riverine woods (Chapin, 1939). It exists in forests as well as woodlands in coastal Kenya, and in bamboo forest on some Kenyan mountains (e.g., Mt. Kenya, Britton, 1980). Highland evergreen forest and juniper woods are occupied in Ethiopia. Its altitudinal range varies as well, for it occurs near sea level and in mountains to 3350 m (Mt. Elgon; Chapin, 1939).

FORAGING HABITS: A major food item of adults is beeswax obtained from beehives that the birds find in various ways. They seem attracted by the presence of bees, they regularly inspect holes and crevices in trees, and they respond by approaching humans who climb or bang on trees (personal observ.). Experiments (figs. 1–3) in Kenya over a ten-day period involved the placing of brown, honeyed comb pieces (i.e., containing comb, honey traces, remains of bee larvae, and other debris of beehives, from an apiarist) at one end of an abandoned hive that had been cut



FIG. 10. Adult Scaly-throated Honeyguide in somewhat submissive posture, showing cleft breast plumage, near experimental hive.

open some nine months before by Kenyan honey gatherers, and pure, clean chunks of whitish beeswax (obtained by S. Njugai from a hive that had been cleared of honey and abandoned by bees after elephants had pushed the tree over, onto the ground) some 25 cm away, at the other end of the opened hive. At least seven different Scaly-throated Honeyguides, and possibly as many as 15 came from all directions over 30 hours of observations. In 104 clearly observed feedings, these honeyguides selected the “honeyed” comb pieces four times, and in the other 100 instances fed on the bare honeycomb (figs. 13–16). The feedings were marked by intense, regular, almost continuous aggressive interactions (figs. 16–17) and cautious, defensive approaches to the honeycomb (figs. 9–12), and many rapid retreating flights from the hive by honeyguides carrying off a large piece of bare comb.

Honeyguides at the hive in the experimen-



FIG. 11. Adult Scaly-throated Honeyguide near experimental hive in full aggressive stance (crown and thigh feathers extended, wings slightly out).

tal situation appeared to defend the food source until so disrupted from feeding (in order to feed, a honeyguide had to face into the hive and thus away from would-be assaults by others) that they flew out, with or without food, or were driven out by another Scaly-throated Honeyguide. We also saw, in three cases elsewhere, a Scaly-throated Honeyguide investigating a tree cavity turn and ward off an incoming, attacking conspecific bird,

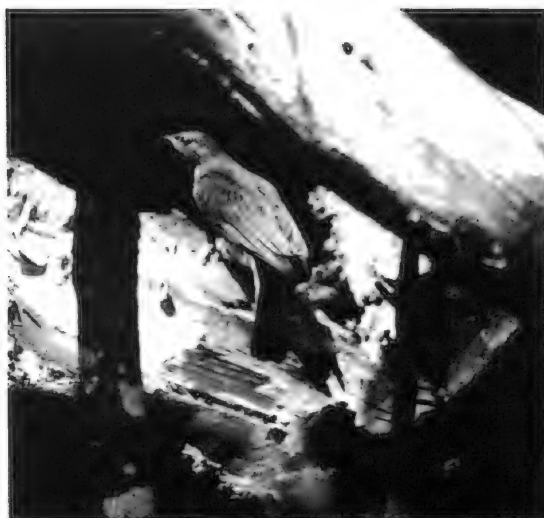


FIG. 13. Adult Scaly-throated Honeyguide at experimental hive. The bird landed at the lower (brown comb) end of the hive, but, tail closed and crown feathers appressed, it prepares to move to the upper, bare comb end of the hive, which a second honeyguide has just left.

i.e., defending a prospective feeding site. Two complex cases at the experimental site illustrate the aggressive nature of encounters there. In one instance two honeyguides were at the hive very briefly together, one at the bare comb on one side, bird A, the other at the



FIG. 12. Stubby-tailed adult Scaly-throated Honeyguide, switching tail as it approaches hive.



FIG. 14. Adult Scaly-throated Honeyguide eating bare wax at the hive.



FIG. 15. Adult Scaly-throated Honeyguide pulling off large piece of comb (from bare comb), before flying off with it.

honeyed comb on the other side, bird B. A had been there when B approached the hive. Bird B then called, gaped, approached bird A, and supplanted it at the bare comb, and A flew off to the canopy of the hive tree. As B began to feed on the bare comb, C, a third individual appeared, and it flew at B, which it supplanted. Bird B flew away, leaving C at the bare comb and A onlooking from the canopy. In another instance a subadult honeyguide was allowed to perch and feed at the honeyed comb by an adult at the bare comb. After some 30 seconds, with a few aggressive, low calls uttered, the adult flew at the subadult, supplanted it, and began to feed on the honeyed comb. The displaced subadult perched momentarily on a nearby branch, then flew to the bare comb. As the subadult commenced feeding, the adult left the honeyed comb and attacked the subadult, supplanting it.

We observed that subadults (or at least one subadult) of this species still uttered begging calls, different from the harsher aggressive notes, and tended to crouch, wave their wings, and beg. In this way a subadult Scaly-throated Honeyguide was able to approach the hive very closely, more so than any adult, while an adult fed at the bare comb. In three instances the subadult actually was able to feed briefly at the honeyed comb in proximity to



FIG. 16. Scaly-throated Honeyguide (above) at bare wax in hive faces off against crouching (appressed plumage) Scaly-throated Honeyguide below.

the adult at the bare comb, before the adult ceased tolerating its presence and displayed at, or attacked it. On three other occasions the subadult perched at the edge of the hive without eliciting attack by a feeding adult, but it did not dare to enter to feed.

Thus, Scaly-throated Honeyguides do act aggressively at or near food sources, both intraspecifically and (see below) interspecifically. In the intraspecific encounters there seems to be a dominance hierarchy of some sort; at least adults are dominant to, but may tolerate somewhat, subadults. Actual dominance in feeding at honeycombs may partly depend on hunger, and on the natural advantage of an inflying bird over an already perched individual, but some birds, e.g., the stub-tailed adult, seemed to supplant and be successful in attacks or defenses more often than not, so a real hierarchy probably exists.⁴

As for location of hives, we cannot comment on Stager's (1967) suggestion that olfaction may play a role in the honeyguide finding the wax, except to state that inquis-

⁴ There exists a definite hierarchy, proven by 1985 studies of 16 color-banded birds at one hive.



FIG. 17. Scaly-throated Honeyguide (above) calling at retreating conspecific bird near hive below.

itive, keen-eyed honeyguides that regularly investigate holes, and are aware of human activities associated with honey-gathering are not apt to need the use of olfactory cues. We have no evidence of honey-guiding by this honeyguide, and we are impressed that the van Somerens, Skead, Chapin, Friedmann, and other long time careful and interested African observers have never observed this species to guide humans or other animals to bees' nests (Friedmann, 1955). Hence, we doubt that this secretive bird regularly, or even occasionally guides humans to honey sources—the few reports cited by Friedmann are unconvincing and require corroboration.

Of course beeswax is not the only, nor even the major, source of food for Scaly-throated Honeyguides. These birds flycatch for insects from perches. They almost always forage individually. Occasionally, a Scaly-throated Honeyguide is seen feeding with other birds in mixed-bird foraging flocks. It gleans from the bark and leaves of trees, moving quietly, usually hidden from the sight of the observer. Much foraging is accomplished low in dense

trees and bushes, or in the understory and middle levels of woodlands.

FOODS: Known items of food, in addition to beeswax, are bees, bee larvae and pupae, aphids, ants, flies, beetles, termites, caterpillars, other insects and arthropods, and some honey, figs, seeds (most likely of fruits), and remains of other unidentified plants.

INTERSPECIFIC BEHAVIOR: Although usually unobtrusive and keeping to cover, this honeyguide is aggressive to other birds that may approach it too closely, and to other honeyguides in feeding situations. We have seen it attack Common Bulbuls (*Pycnonotus barbatus*) that were watering, and on eight occasions, Tree Pipits (*Anthus trivialis*), which have a white-edged tail, when the pipits were in flight.

In our experimental situation in central Kenya, described above (see Foraging Habits), Scaly-throated Honeyguides consistently dominated Greater Honeyguides (*Indicator indicator*), Lesser Honeyguides (*I. minor*, fig. 18), and an apparent Pallid Honeyguide (*I. meliphilus*), keeping them from beeswax by



FIG. 18. Scaly-throated Honeyguide (upper left) causing Lesser Honeyguide (lower right) to flee from near hive.

actively attacking and supplanting them. Although Lesser Honeyguides frequently were noted about the beeswax site, they were kept from it for over ten days by Scaly-throated Honeyguides; one Lesser Honeyguide managed to dart in and secure wax only twice. On one occasion three Scaly-throated Honeyguides were actively interacting in the canopy over the hive, and a Lesser Honeyguide perched and fed for 30 seconds on the bare comb before being driven away by one of the Scaly-throateds. On the other occasion a Lesser Honeyguide darted to the honeyed, brown comb bits and managed to grab several pieces before a Scaly-throated Honeyguide present at the (bare) wax threatened it, causing the Lesser to fly off. Several chases of Lesser Honeyguides by Scaly-throated Honeyguides near this site also were noted; when being pursued, the faster Lesser Honeyguide at least twice returned the attack, and the two birds flew off calling, engaged in a flying encounter.

Greater Honeyguides approached the experimental site more often (figs. 20–21) than did Lesser Honeyguides, probably because their habit of perching conspicuously on dead branches or the tops of trees generally kept them from conflict with the Scaly-throated Honeyguides. The latter, more numerous, stayed inside the trees and at lower levels, only occasionally venturing into the open. At least three Greater Honeyguides, an adult male, an adult female, and a subadult male were seen in trees near the experimental hive over a ten-day period. The subadult never ventured into the hive tree, where Scaly-throateds usually were present, and it was chased from a nearby tree by one Scaly-throated. The adult Greater Honeyguides did go to the hive tree, but frequently were attacked and driven from the vicinity. On only four occasions did the (or an) adult male reach the hive, and manage to eat some of the bare wax comb. The (or a) female entered the hive twice, once going briefly to the bare comb,

and once, harried by a Scaly-throated, to the brown, honeyed comb. In the hive tree we observed ten supplanting attacks by several Scaly-throated Honeyguides on the male Greater Honeyguide, all of them successful. Likewise, the six attacks on the (or a) female Greater Honeyguide by a Scaly-throated Honeyguide were successful. On a few occasions the Greater Honeyguide returned to a nearby tree after being driven off, but only to perch and watch. On only one occasion did we see an attack by a Greater Honeyguide on a Scaly-throated Honeyguide—in this case, a female Greater flew at a subadult Scaly-throated perched beside the hive, but the latter held its position, smashed at the female Greater with bill and wings, and caused the female to fly away. These data strongly suggest that *I. variegatus* is dominant to *I. indicator*, females of which may be more aggressive than are males (see account of *I. indicator*).

ACOUSTIC DISPLAYS: Young utter a low, husky “chess-chess-chess-” call with notes at four or five per second (Dowsett-Lemaire, *in litt.*; 1983), and when near fledging, a trill, “foy-foy-foy-” (Dowsett-Lemaire, 1983, p. 72). Birds held in the hand after capture in nets utter a sharp squawk. Various interactive calls have been recorded on tape, as when two birds (of unknown sex) have an encounter at a honeycomb source (fig. 6E). One interactive aggressive note is a buzzy “zh-zh-zh” or “tzha-tzha-” with sound concentrated at 5 to 8 kilohertz. Sonographically the notes are unformed, with noise over a wide spectrum of pitch. The notes usually last 0.5 to 0.1 second with variable intervals of 0.02 second and more between notes, and are uttered at up to 10 per second. Occasionally the sound is continuous, a “zzzzh” over 0.25 to 0.35 second, then breaking into shorter notes at irregular intervals (fig. 6G). Even shorter “dz” notes in series are but 0.01 to 0.02 second in duration, given in bursts at 13 to 20 notes per second at the same range of pitch as the “zh-zh” notes. These may speed up and continue for 2 or more seconds, as a “dz-dz-dz-dz-dz-zzzzzip.” Intermediate “zh” and “dz” notes also occur. Interacting birds may utter either of these calls, or one may give “dz-dz-dz-” calls continuously as the second bird repeatedly calls “zzha, zzha” in groups of 1

to 3 notes at variable intervals. The second, chattering call (fig. 6F, H) of these two calls is somewhat like the guiding chatter of the Greater Honeyguide (*I. indicator*), but does not appear related to honey-guiding activity. A third, less frequent aggressive note is a more discrete, formed double “tza-dat” call (fig. 6I), with a buzzy beginning, dropping from an initial peak, breaking and rising to 1 to 1.3 kilohertz, followed by a clearer second element ending in a sharp peak at 1.7 kilohertz. These show overtones, and are 0.18 to 0.2 second in duration, uttered in series of about 2 per second.

A whistling call of 1–6 notes at about 2 per second, and easily mimicked, is a “foyt-foyt-foyt-.” Its function is unclear, although humans whistling it can attract Scaly-throated Honeyguides. The song, or song trill (fig. 19A, B), is a churring series that varies even in the same bird from a froglike croaking sound to a loud, vibrant police-whistle-like series (Friedmann, 1955). The song lasts 2 to 4 seconds, and commences with longer notes uttered at a rate of 18 to 20 per second, then changes over, becoming louder, giving way to a rapid trill at 40 to 42 notes per second. Songs of 3.28 to 3.38 seconds in duration contained 115 to 121 notes (central Kenyan birds). This song is uttered from beneath the canopy of trees or bushes, and usually is considered to be delivered from a very specific song perch (Friedmann, 1955; Ranger, 1955). We have observed a singing Scaly-throated Honeyguide more or less following several Nubian Woodpeckers (*Campethera nubica*) about, and singing from seven perches, including one on a herbaceous plant a meter from the ground at the edge of a woodland. Playback also tends to draw singing birds closer to the playback recordist, the honeyguide singing at one site, moving, singing at another site, and so on, until singing overhead. It is inconceivable that these sites all represent distinct song perches regularly used by territorial honeyguides. As in the case of the Lesser Honeyguide, the situation may vary geographically in regard to song perches. As many as 76 songs may be given in 90 minutes, with singing particularly early in the morning (even before daybreak), but also at intervals during the day (Ranger, 1955).

VISUAL DISPLAYS: These are poorly known.

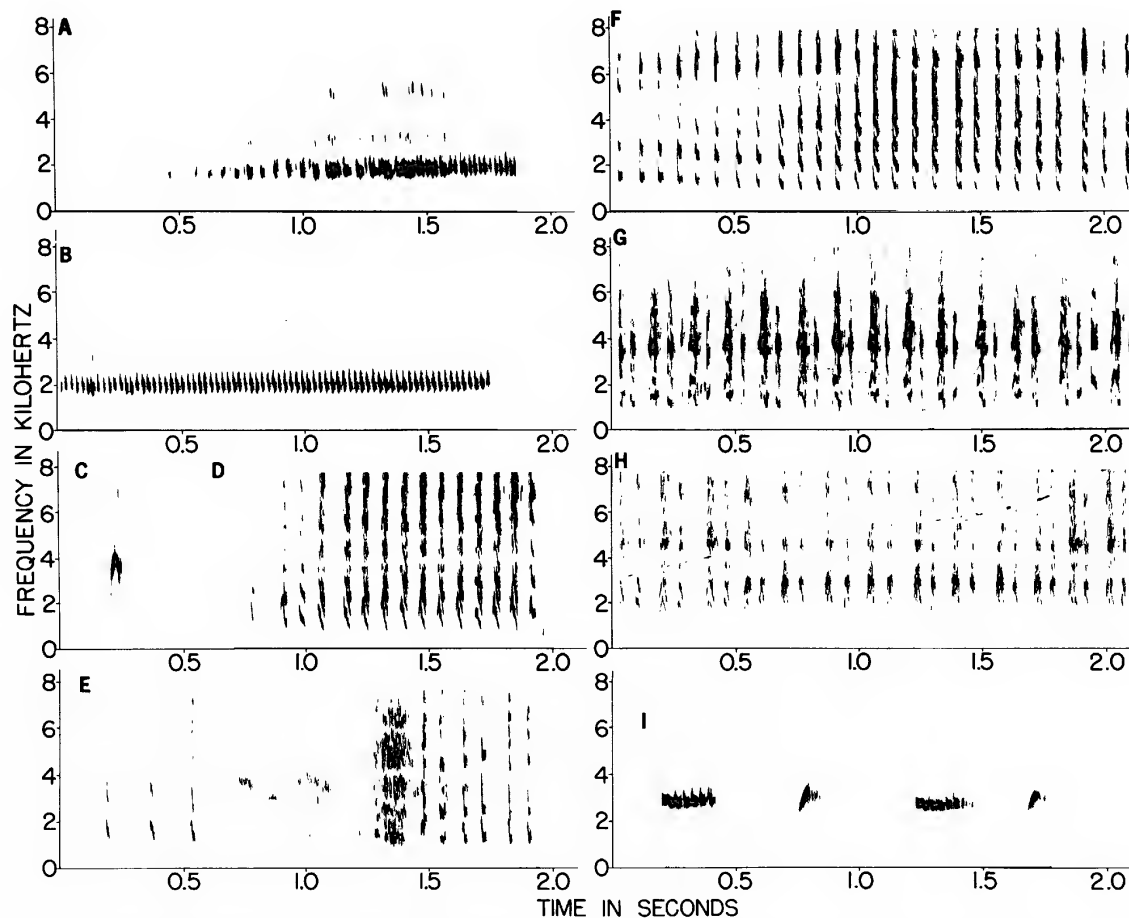


FIG. 19. Vocalizations of Scaly-throated and Greater honeyguides in wide-band sonograms. A, B. Full song (trill) of *Indicator variegatus*, Dec. 12, 1983 at Ol Ari Nyiro, Kenya. C. Peep call of *Indicator indicator*, August 1968, Ol Ari Nyiro, Kenya. D. Mixed piping and squeaking notes of *I. indicator* in interactive trill, Dec. 17, 1983, Ol Ari Nyiro, Kenya. E. Three piping notes, two faint chatters, a noisy chattering note, and six squeaky piping notes during interaction at experimental site by male *I. indicator* at *I. variegatus*, Dec. 17, 1983, Ol Ari Nyiro, Kenya. F. Chatter trill form of guiding call of male *I. indicator*, showing only slight tendency to paired notes, Dec. 17, 1983, Ol Ari Nyiro, Kenya. G. Double-noted guiding call of male *I. indicator*, August 1968, Ol Ari Nyiro, Kenya. H. Double-noted guiding call of male *I. indicator*, Jan. 3, 1982, Akagera Park, Rwanda. I. Terminal two sets of "burr-wit" or "tor-vik" song of 10 sets by male *I. indicator* Aug. 26, 1980, Dzalanyama Mountains, Malawi.

Interacting Scaly-throated Honeyguides gape in a horizontal posture with head extended at an antagonist; the wings and tail are flicked frequently and there are side-to-side body and head movements as antagonists approach one another. The throat feathers may be ruffled and could serve to highlight the scaly throat in adults showing this feature. Flight displays also occur, with fluttering—whether by aggressive or courting adults is unknown. The tail is spread often, not only during encoun-

ters but at intervals as a honeyguide moves about, foraging or watching host species. These honeyguides outfly most of their host species, and often turn upon them when chased, ending up perching or supplanting the hosts.

HOSTS: The known hosts of this widespread honeyguide are surprisingly few. Verified are the Black-collared (*Lybius torquatus*) and Whyte's (*Stactolaema whytii*) barbets, and the Yellow-rumped Tinkerbird (*Pogoniulus bi-*

lineatus) among capitonids, and the picid Nubian (*Campethera nubica*), Golden-tailed (*C. abingoni*), Olive (*Dendropicos griseocephalus*), Gray (*D. goertae*), and Cardinal (*D. fuscescens*) woodpeckers (Friedmann, 1955, 1958a; Dowsett-Lemaire, 1983). The record of the tinkerbird, which excavates a cavity so tiny as to make entry of a female Scaly-throated Honeyguide very difficult at best, is accepted from van Someren's notes (in Friedmann, 1955, and especially Friedmann, 1958a, p. 311, *contra* Dowsett-Lemaire, 1983, p. 74). Excited, repeated responses of a Scaly-throated Honeyguide to playback of the voice of the Green Tinkerbird (*Pogoniulus simplex*, Short and Horne, 1979, pp. 3–5) reinforce the van Someren observations, and indicate that this honeyguide somehow manages to get its egg into tinkerbird nests (see below).

We consider as unsubstantiated the reports of these hosts (Friedmann, 1955): Horus Swift (*Apus horus*); White-cheeked Barbet (*Stactolaema leucotis*); Crested Barbet (*Trachyphonus vaillantii*); and Yellow-throated Petronia (*Petronia supercilialis*). The two barbets among these are likely to prove hosts of this honeyguide. Our observations of playback responses of *I. variegatus* to voices of the Green Tinkerbird, Green Barbet (*Stactolaema olivacea*, see Short and Horne, 1979, p. 5), Brown-breasted Barbet (*Lybius melanopterus*), Green-backed Woodpecker (*Campethera cailliautii*), and Bearded Woodpecker (*Dendropicos namaquus*) suggest these species as possible hosts.

It is clear that, as with the Lesser Honeyguide (*Indicator minor*) and unlike the Greater Honeyguide (*I. indicator*), the preferred hosts of *I. variegatus* are barbets and woodpeckers. There are no data on host specialization by individual female Scaly-throated Honeyguides.

TERRITORIALITY AND BREEDING HABITS: Details concerning territoriality and its mating system are known only from some South African studies (Friedmann, 1955; Ranger, 1955). Presumed males maintain traditional (long-term, occupied for as long as 26 years, although not likely by the same bird) song perches on branches beneath the canopy of trees, from which they sing at intervals over the breeding season. In southern Africa the

period of singing mainly is from August to December, with a declining amount of song thereafter, to April. Outside of southern Africa the singing period is much shorter, and more variable. Furthermore, even within southern Africa songs sometimes are uttered from perches other than the traditional ones, and in Kenya moving birds may sing from diverse perches, even in bushes in grassy areas out of woodlands (personal observ.). Singing may come from two birds as close to one another as 230 to 250 m.

It is presumed that females come to the males' calling or stud sites (Friedmann, 1955). There are no observations of courtship, nor has copulation been observed.

Scaly-throated Honeyguides that are attracted to sources of beeswax obviously cross any existing territorial borders, since one can observe up to seven about such a site (personal observ.). The fact that there appears to be a dominance hierarchy at feeding sites, and that immature birds achieve some success in staying close to these sites without being driven away suggest that the hierarchy may be sex-related and related to "territory," that is, local, perhaps territorial, individuals may be dominant, although not so dominant as to maintain exclusive control over the food source.

Singing males (determined by collecting) actively follow vocal, interactive (e.g., males interacting with females, and even adult-juvenile interactions) individuals of host species. We watched one male singing in sporadic bursts following a pair of Nubian Woodpeckers that were accompanied by a noisy, begging young woodpecker. The honeyguide sang in view of the woodpeckers, moved with them, and came to our playback of their interactive calls. We obtained such a male Scaly-throated Honeyguide that proved to have large testes, after it followed Nubian Woodpeckers, and just after it had sung over us in response to our playback of Nubian Woodpecker calls. A Lesser Honeyguide (*I. minor*) had followed the same woodpecker pair, even more closely than had the Scaly-throated Honeyguide (in fact, *minor* flew with, was attacked by, and attacked the woodpeckers several times as it placed itself beside them). The Scaly-throated Honeyguide once attacked the Lesser Honeyguide and chased

it, and was chased by it in return. We suggest that at least some breeding male Scaly-throated Honeyguides may have a territorial system that is seasonal, and based upon breeding pairs of its hosts that are defended from other Scaly-throated Honeyguides, as in the case of Lesser Honeyguides, for which we have more evidence (Short and Horne, 1983).

There are no data on the pair relations and activities of the female Scaly-throated Honeyguide in entering the cavity nests of its hosts. Dowsett-Lemaire (1983) found that scattered apparently female Scaly-throated Honeyguides occurred high on Malawi's Nyika Plateau, laying in nests of Olive Woodpeckers in areas where no songs were heard or singing posts of male honeyguides were located. Females are not known to remove or destroy eggs of the hosts, although Dowsett-Lemaire (1983, p. 74) noted one possible such case. Occasionally this honeyguide (same individual?) may lay more than one egg in a host's nest, and there even is a report (Friedmann, 1955) of a Whyte's Barbet nest bearing three eggs of that barbet and, supposedly, three eggs of the Scaly-throated and one egg of the Lesser honeyguides. At least two eggs and probably more are laid by a female. A continuously chattering Scaly-throated Honeyguide perched with tail clinging to the nest entrance of a pair of Olive Woodpeckers may have been attempting to lay (Dowsett-Lemaire, 1983).

Laying occurs in May in Kenya, in September to October in Malawi, in October in Zambia, in September to January in Zimbabwe, in December in Transvaal, and in October in Natal (Benson et al., 1971; Benson and Benson, 1977; Stuart Irwin, 1981; Brown and Britton, 1980). Other indications of breeding we have gleaned from specimens and the literature suggest breeding in November and January in Ethiopia; February in Sudan; September and February in Uganda; May, June, and January in Kenya; August to October in Mozambique; May and July in eastern Zaire and October to December in southern Zaire; April and July to October in Malawi; February and June in Angola; and October to December in South Africa. Reflecting earlier breeding are the many records of juveniles; we emphasize that it is uncertain

(and probably variable) how long the juvenal plumage is retained, but this is not apt to be longer than three to four months after hatching. Southern African juveniles date from October to February. Such birds are known as follows: December, March, and June in Ethiopia; February and March in Sudan; February and May (nestlings) and April, June, July, August, and November in Uganda; June to July nestlings, May to June fledglings, and others from all months except August in diverse parts of Kenya; July, August, November, and March in northern and central and February in southern Tanzania; and January, April, October, and December for Zaire. The molt occurs late in the breeding season and immediately thereafter, and all data that are available are in accord with the seasonality indicated by the laying, breeding, and young of this honeyguide that have been discussed.

The incubation period is calculated to be approximately 18 days by Dowsett-Lemaire (1983). The young honeyguides have the typical *Indicator* bill hook, and they usually, if not always, destroy the eggs or occupants of the host's nest (the one supposed record of a young of the host, an Olive Woodpecker, with a young Scaly-throated Honeyguide is subject to doubt, see Sclater and Moreau, 1932; Friedmann, 1955; and Dowsett-Lemaire, 1983).

Young are fed insects and (by barbets) fruit, the foods normally fed to their young by the foster parents. Feeding occurs up to 45 times in eight hours (Dowsett-Lemaire, 1983). The young honeyguides, according to that author, fledged in 27 to 35 days, and once leaving the nest, the young honeyguide does not reenter it. Rather, it perches and begs from a site in a small area about the nest, in the case of Olive Woodpeckers as the host. Dowsett-Lemaire (1983) noted the efforts of the woodpecker foster parents to get the young honeyguide back into the nest to roost for the night, without success. That author failed to locate young Scaly-throated Honeyguides being fed beyond the day of fledging, which, with our observations of the Lesser Honeyguide, suggests that newly fledged honeyguides very rapidly, if not instantly, become independent upon fledging. Nevertheless, fledged Scaly-throated Honeyguides have been observed being fed by Whyte's and



FIG. 20. Adult male Greater Honeyguide (*Indicator indicator*) above hive, looking up at Scaly-throated Honeyguide.

Black-collared Barbets; Yellow-rumped Tinkerbirds; and Gray, Olive, Bearded (Taylor, 1983), and Cardinal woodpeckers. Van Someren (1956) reported the enlargement of the nesting cavity by a pair of Yellow-rumped Tinkerbirds hosting a young Scaly-throated Honeyguide, apparently in order to enable the fat young honeyguide to leave the nest (its mother obviously must somehow have entered the tiny hole leading into the cavity).

The only information available on behavior of independent juvenile Scaly-throated Honeyguides comes from our Kenyan studies of honeyguides at beeswax sources. We found that the single Scaly-throated Honeyguide in juvenal plumage among the dozen or so that frequented the beeswax was much more successful than most of the adults in remaining close to the beeswax, if not in feeding on it. That is, its sporadic begging behavior, crouching in submission, and probably its feather markings enabled it to bypass the dominance hierarchy established among the adults. It was allowed to approach adults more closely than were other adults, and even to perch and feed at one end of the experimental hive containing beeswax while another adult was present, much less often eliciting an attack and pursuit by the adults than occurred when one adult tried to approach the hive while another adult was present. Also, when three or four birds, including the juvenile, were present and interacting near the hive, the juvenile largely was ignored, the adults



FIG. 21. Adult male Greater Honeyguide trying, without success, to reach experimental hive that was occupied by Scaly-throated Honeyguide.

attacking and pursuing one another, often to the advantage of the juvenile that was able to get to the hive, and make off with some wax in the absence of adults.

Indicator indicator (Sparman)
Greater Honeyguide (figs. 20–21)

RANGE SUMMARY: This honeyguide occurs from the trans-African Sahel belt (southern Mauritania to northern Ethiopia) south to northeastern Namibia, northern and eastern Botswana, and the Cape Province and Natal, South Africa, avoiding true deserts, extensive grasslands, and forests such as the main mass of the Congolese forest (it does not reach the forested coast of West Africa). Its behavior and use of conspicuous perches make it the best known of the honeyguides.

HABITAT: Greater Honeyguides frequent bushlands, wooded grasslands, and open woodland, and to a lesser extent, forest edges, dense woodlands, riverine woods, and scrub desert. They are more common in open, dry situations with scattered trees than in forested or densely wooded areas. Where the habitat is open the species occurs up to 3000 m in elevation (East Africa, Britton, 1980), but it is more common below 2000 m. It does

not shun habitation, but occurs in cultivated regions and even in eucalyptus groves. Because beeswax is a favorite food, it is apt to be found where bees are abundant.

FORAGING HABITS: The Greater Honeyguide is the only regularly guiding member of its family, attracting attention of people and certain other mammals, mainly the Ratel (*Mellivora capensis*), and guiding them to active beehives. This well-known behavior is at least partly influenced by learning, for in suburban and village areas where people no longer seek honey from the hives of wild bees, the Greater Honeyguides infrequently or never guide, becoming less conspicuous thereby (Friedmann, 1955). The guiding has been described in great detail by Friedmann, and we only summarize it here. One first notices a persistent chattering call and notes the bird, which may be of either sex (immature-plumaged birds guide as well). Its tail flits apart and the bird bobs, looking at the prospective honey-seeker. It then moves in undulating flight, fluttering as it flies a variable distance in a certain direction (toward a hive), perches again, and incessantly calls. If followed the bird repeats the guiding a number of times until, perhaps a kilometer or more from the starting point, the hive is at hand. The honeyguide's final flight to the immediate vicinity of the beehive is followed by its silent scrutiny—it depends upon the person (or mammal) being guided to observe the bees and to attempt to get the honey. While the activity goes on the bird perches quietly, or may move about to alternate perches. Traditionally tribal peoples leave a piece of honeycomb conspicuously placed out for the honeyguide, which moves to the hive and commences feeding when the honey-hunters have gone. If no one follows the bird initially, the honeyguide may call at frequent intervals, for up to 5 minutes constantly at one burst. Its attempts may last an hour or more, as it moves from tree to tree around one (personal observ.).

Obviously the honeyguide must have knowledge of the location of one or several active beehives. No one has described how the birds find a hive, but visual clues (bees moving in numbers, or a mass of bees in one place) must play a major role. Whether or not the hives to which the Greater Honeyguide

guides pose special problems of entry for the bird is unknown. Clearly the Greater Honeyguide, like all its congeners, must locate active and inactive hives on its own, to obtain wax. It may be that the large size of the Greater Honeyguide makes it difficult to gain entry to some hives (however, the much more secretive and usually nonguiding *I. variegatus* is virtually the same size). Or, it may feed to a greater degree than other congeners on the larvae and eggs of bees, requiring active hives.

In addition to beeswax, and the bees, their eggs, and larvae that are taken accidentally or by choice when it feeds on the wax comb, the Greater Honeyguide flycatches from perches to secure insects, probably its primary food. Honeyguides may participate in interspecific foraging flocks that are a common feature in African woods. Several Greater Honeyguides may associate in these flocks, and in flycatching, as well as gathering at wax sources; immature birds especially are liable to form loose associations. At wax sources we have noted aggression, adult females being dominant to adult males. The honeyguides may forage about large grazing and browsing mammals, flycatching for insects that are disturbed by the mammals. We also have seen them follow woodpeckers foraging in trees, flying down to pick off the insects flushed by the woodpeckers' movements. Their occasional, reported feeding on eggs of other birds (Friedmann, 1955) may be the reason why they sometimes are mobbed by small birds that are not their hosts.

FOODS: The main foods are insects including diverse larvae, beetles, ants, termites, the pupae, larvae, eggs and adults of bees; and beeswax. A. W. Diamond (*in litt.*) maintained captive Greater Honeyguides for up to six months on a diet of chopped meat and hard-boiled eggs. In feeding trials with honeycomb, Dr. Diamond found the captive birds first sought out larvae of the bees, then ate the wax. The honeyguides on occasion eat eggs of other birds. The young honeyguides are fed on insects, fruits, and the other foods normally fed to their own nestlings by their foster parents. It has been assumed that the digestion of wax by the Greater Honeyguide is through the means of aerobic lipolytic bacteria (Friedmann and Kern, 1956), although the action of aerobic bacteria in the confines

of the digestive organs poses some problems according to Dr. Diamond. Enzyme action or the action of cerolytic yeasts are other possibilities for digestion of beeswax by the honeyguide (Friedmann, 1955). It is certain that the honeyguide cannot exist for long on a diet solely of beeswax, as in the case of Lesser Honeyguides that died in about one month of feeding only on beeswax (Friedmann, 1955, p. 75).

INTERSPECIFIC BEHAVIOR: Because of their conspicuous perching and flycatching, as well as their aggressiveness, Greater Honeyguides frequently have aggressive encounters with nonhost species. The African Drongo (*Dicrurus adsimilis*) may attack a perched Greater Honeyguide, as may rollers (*Coracias* spp.), and almost inevitably the Greater Honeyguide returns the attack (see fig. 6J). It does not readily relinquish a perch unless a bird is much larger (e.g., a hornbill, *Tockus* spp.), or indeed is a predator. The Greater Honeyguide sometimes approaches a recordist playing back the voice of the Lesser Honeyguide (personal observ.). It may briefly chase a Lesser Honeyguide that it encounters, the latter being faster and more maneuverable. At sources of beeswax we have noted that it consistently is dominant to smaller honeyguides, such as *I. minor*, but invariably is driven away, supplanted, or kept from wax by Scaly-throated Honeyguides. We often saw Greater Honeyguides simply avoid proximity to *I. variegatus* and the wax when the latter was present. At our Kenyan study site (see above discussion of *I. variegatus*) we observed ten supplanting attacks of *I. variegatus* on males of *I. indicator* (figs. 20–21), six of *variegatus* on females of *indicator*, one of *variegatus* on a subadult male of *indicator*, and one attack of a female *indicator* on a subadult *variegatus*—this last failed, the *variegatus* holding its position, then chasing the *indicator* away (personal observ.). It should be noted that Friedmann (1955, p. 35) found no possessiveness in honeyguides he studied, mentioning the coming together of several honeyguides, even of *I. minor* with *I. indicator*, without noting aggression. Our observations, in contrast, show a strict dominance hierarchy of honeyguide species (*I. variegatus* over *I. indicator* over *I. minor*), and of the sexes and age groups intraspecifically (female

indicator over male *indicator* over subadult *indicator*). Such behavioral differences may be seasonal, or geographical, as Friedmann's studies largely were in southern Africa.

ACOUSTIC DISPLAYS: The young Greater Honeyguides utter a series of chattery notes that are loud and irregular, bearing resemblance to the guiding call. They pull the head back and tilt the bill upward as they call at 5 to 10 notes per second. Fry (1974) considered these calls to be vocally convergent upon those of bee-eaters (specifically *Merops bulcocki*), but this honeyguide has many, diverse hosts, and the voice of its young is not apt to resemble convergently any one more than others. A. W. Diamond noted (*in litt.*) that the begging call of one honeyguide sounds like two or more calling individuals, and the loud calls may elicit feeding at greater rates than a lone nestling otherwise might obtain.

Mechanical sounds include wing noises made during presumed courtship flights, so-called drumming, and a "brrr" sound made by a male near a female. The drumming sound, likely made with the wings, occurs as a male circles back and forth, dipping as it circles, giving a "Bvooommm" or "whoosh" sound, followed after a pause by another, and so on (see under Visual Displays below). The tail is closed when this flight display occurs, and the display itself has not been observed frequently (see Friedmann, 1955). Courting individuals also snap the bill occasionally.

A squeaky, short note (Short and Horne, 1979, fig. 2) forming a peak sonographically and having overtones is an interactive, aggressive call similar to squeek calls of congeners. This call, rendered "tych," "tyek," or "yeh" is uttered in conflicts with other species (e.g., Green Barbet, *Stactolaema olivacea*), and may be heard between a male and female Greater Honeyguide. In figure 6J are shown a series of squeaky notes uttered by a male *I. indicator* chasing an African Drongo. A single piping, peep note with a peak at 4 kilohertz, given in 0.04 second also is heard during interactions (fig. 19C). This resembles the "vik" or "wit" note of the song (see below). Irregularly given in series of five or so per second, these piping notes mark encounters of some intensity, such as one with Green Barbets (see Short and Horne, 1979, fig. 1). A more aggressive, trilling series of notes (fig.

19D) combine the form of squeak and piping notes, given at 12 to 14 notes per second. These somewhat resemble the interactive chattering calls and the guiding call (see below), but the notes are more piping with a peak. Possibly this is the "screaming-chattering" that Ranger (1955, p. 78) heard from a copulatory pair. Other interactive series combine features of these various notes (fig. 19E). Hissing notes that we have not heard are reported from intensely aggressive birds by A. W. Diamond (*in litt.*).

The guiding call is a long, irruptive series of chattery notes, varying from a regular trill (fig. 19F) to a less double-noted series (fig. 19G, H). The more regular, noisy chatter seems to us to occur in the presence of a second honeyguide, or when the calling bird is disturbed (as near our experimental beeswax site in Kenya). Notes are short (0.01 to 0.015 second) with a dropping tendency but much noisy sound at varying frequencies, delivered at 12 to 14 per second. The double-noted chatter is more typical of guiding calls, but these may vary with the intensity of the honeyguide's reaction to prospective followers over time. At 14 to 16 notes per second the pairs of notes consist of a longer, usually louder, first note, and a shorter, softer second note, imparting the insistent quality to the guiding call. There may be short bursts of notes for five or six seconds, followed by a pause, or a bird may call continuously for several minutes. The call may be rendered "churra-churra-churra-churra-" for the double-noted version, or "chur-chur-chur-chur-" for the simpler chattery trill. Males, females, and juveniles may give the guiding call, and guide.

The song, variously termed the "vik-tor," "wit-burr," or "wit-cheer" call, is uttered so far as is known by males, often from traditional song perches (see territoriality below). Most songs we have heard end in a "wit" or "vik" note (fig. 19I), as Friedmann (1955, p. 121) suggested, but we have not analyzed a sufficient number of fully complete songs (the initial note, probably usually a "burr" or "tor" note, is soft and the song is uttered at 40- to 80-second intervals, hence it is difficult to record its start) to state that the full song is indeed a "tor-vik" or "cheer-wit" rather than the usually ascribed reverse. Indeed,

Ranger's (1955, p. 72) observations suggest that the song regularly starts with a soft "burr" and ends in a "wit." The "wit" is sharp and fast, at 3 to 3.5 kilohertz, and often rises over its 0.02 to 0.04 second duration. The slightly lower pitched, buzzy "burr," 0.1 to 0.22 second in duration, consists of a long initial and two to six following elements, lending emphasis to the sharper "wit," which follows the "burr" in 0.25 to 0.38 second (the next "burr" is about 0.4 second after the "wit," and this timing varies more, so the "burr-wit" version more accurately describes the song). The calls are audible for up to 825 m (Ranger, 1955). A call takes six to 11 seconds, about a second per pair of "burr-wit" notes, with six to 11 pairs per song. During the peak period of singing the song is uttered at about one minute intervals almost continuously for several hours, especially in the morning, but also in the afternoon and sporadically through the day. There may be long pauses when the male shifts calling sites. Late in the season the calling intervals diminish and ever greater intervals pass without songs, until they cease altogether (Ranger, 1955; see below).

VISUAL DISPLAYS: These need thorough study, especially in view of the marked sexual difference in plumage that is not found in other honeyguides. Aggressive birds hunch the back with (golden) leading edges of the wings raised, the neck arched and the bill open. In more intense aggression the honeyguide stretches its open bill at an antagonist and hisses (A. W. Diamond, *in litt.*). A female soliciting copulation near a male's song perch flicks its wings about, and its tail as well (Friedmann, 1955, p. 128; Ranger, 1955, p. 78). It then stretches forward, crouches, and the approaching male alights on her, stretching his chin and neck onto her head and copulating with wings fluttering and her tail turned to the right (Skead, 1951; Friedmann, 1955). The male fluffs its crown feathers at times, puffs its body, arching it, and moves about the female with beating wings and spread tail, as in turkeys (*Meleagris gallopavo*).

Ranger (1955, p. 78) described a copulation differing in that the male seemed to grasp the upper neck of the female, one or both then gave a screaming-chattering call throughout the end of copulation, they then

flew in a chasing flight, and there followed two "drumming" flight displays (see discussion above under Vocal Displays) by the male over the area.

The notes of A. W. Diamond also are of great interest regarding breeding and display, and we paraphrase from his unpublished notes on observations of October 30, 1977, in Kenya: Male honeyguide began singing about 10:15. At 12:05 I went to watch him, and first saw a female on a branch of an *Acacia xanthophloea*. She kept up a constant wing-flicking, also raising and slightly spreading the tail, but not showing much of its white edges. At this point the male was about 4 m from her, perhaps 2 m above her. The singing male raised its head, stretched and inflated its neck, with bill at a 60 degree angle to the horizontal, and open. In about 5 minutes the male flew to the female, tried landing on her back, but sat upon her head and she flew to about 10 meters away. Another male singing, female wing-flicking bout ensued, ending with another attempt at copulation, the male pecking at the female's nape; the copulation apparently was unsuccessful. Again, after 5 minutes, this was repeated, the male finally landing atop the female, gripping her back with his bill, and staying on her for 10 to 15 seconds until she apparently lost her balance; with some squawking notes both fell, locked together, into long grass below the tree. After 30 seconds the male flew up from the grass into the air, then flew in a circle about 50 meters in radius, very deliberately, making loud "whoosh, whoosh" noises with his wings. He did this three times before flying into another tree, giving me a good view from below—the noise definitely came from the feathers, and was not vocal. A few seconds later the female flew up and silently went off in a direction away from the male, this at about 12:30.

HOSTS: Definite hosts number 39 species, while evidence is unsatisfactory to verify reports for 11 others. Most are hole-nesting birds, or build deep nests (the white eggs of the honeyguide would be conspicuous in shallow cup nests). Friedmann (1970) noted that 47 of 161 cases of which he knew involved bee-eaters, fewer than one-third of the total number. The hosts include 17 coraciiform birds (eight are bee-eaters), nine pici-

form species, and 13 passerines (especially swallows and starlings, which nest in holes, or in covered nests, or in mud nests in dark places). The Hoopoe (*Upupa epops*) is a common host. Bee-eaters include: the Cinnamon-chested (*Merops oreobates*), Swallow-tailed (*M. hirundinaceus*), White-fronted (*M. bullockoides*), Carmine (*M. nubicus*), Little (*M. pusillus*), Little Green (*M. orientalis*), Madagascar (*M. superciliosus*) and Bohm's (*M. boehmi*). The Abyssinian Roller (*Coracias abyssinica*) is the only coraciid (Parker, 1966). There are three wood-hoopoes (Scimitarbill, *Phoeniculus cyanomelas*, Abyssinian Scimitarbill, *P. minor*, and Green Wood-Hoopoe, *P. purpureus*), and four kingfishers (Pygmy, *Ispidina picta*, Chestnut-bellied, *Halcyon leucocephala*, Striped, *H. chelucuti*, and Brown-hooded, *H. albiventris*). Definite barbet hosts are the Pied (*Tricholaema leucomelaina*), Black-collared (*Lybius torquatus*), and Crested (*Trachyphonus vaillantii*). Woodpeckers are the Rufous-necked Wryneck (*Jynx ruficollis*), Nubian Woodpecker (*Campethera nubica*), Golden-tailed Woodpecker (*C. abingoni*), Knysna Woodpecker (*C. notata*), Tullberg's Woodpecker (*C. tullbergi*), and Gray Woodpecker (*Dendropicos goertae*). Other groups represented by more than one species are: swallows, White-throated (*Hirundo albigularis*), Rufous-chested (*H. semirufa*), Larger Striped (*H. cucullata*), and Banded Martin (*Riparia cincta*); starlings, Pied (*Spreo bicolor*), Red-shouldered Glossy (*Lamprotornis nitens*), and Blue-eared Glossy (*L. chalybeus*); thrushes, Cape Anteater Chat (*Myrmecocichla formicivora*) and Anteater Chat (*M. aethiops*); and sparrows, Grey-headed (*Passer griseus*), and Yellow-throated Petronia (*Petronia superciliaris*). Other hosts are the Black Tit (*Parus niger*) and Scarlet-chested Sunbird (*Nectarinia senegalensis*). The Cardinal Woodpecker (*Dendropicos fuscescens*) is a likely host. Other reported hosts, records for which need corroboration (non-hole-nesters are unlikely) are: Yellow-rumped Tinkerbird (*Pogoniulus bilineatus*), Red-fronted Tinkerbird (*P. pusillus*), Cape Bulbul (*Pycnonotus capensis*), Zanzibar Sombre Greenbul (*Andropadus importunus*), African Drongo (*Dicrurus adsimilis*), Tropical Boubou (*Laniarius ferrugineus*), Black-backed

Puffback (*Dryoscopus cubla*), Black-headed Oriole (*Oriolus larvatus*), Cape Rock Thrush (*Monticola rupestris*), and Violet-backed Starling (*Cinnyricinclus leucogaster*).

TERRITORIALITY AND BREEDING HABITS: Individual birds probably cover wide areas, and territoriality has generally not been established. Even in southern Africa, where song perches are traditional for 22 years or more, more than one male may use the same song perch alternately and may sing simultaneously from adjacent sites that both have used previously (Ranger, 1955). Little or no aggression is evident from the literature, suggesting that territorial defense, if there is any territory, is minimal. However, at our Kenyan experimental site we never observed more than one adult male, one adult female, and a subadult male in the area at any given time. Furthermore, the female supplanted the male, and both kept the subadult male from the vicinity of the beeswax. Although our observations may not bear directly on territoriality, there is good evidence for aggression that is associated with such, and these honeyguides are aggressive. A. W. Diamond (*in litt.*) reports that caged and neighboring wild males are regularly aggressive to one another.

Each male has several calling sites in the South African birds that Ranger (1955) and Friedmann (1955) observed. Calling at these sites was regular from September to December, with earlier singing in August, and tapering off in January and February. Ranger noted that, although there are primary and secondary sites, the males may call from other than the main song perches. As discussed under Visual Displays (above), it is to these song perches that females come to mate. Ranger's evidence (1955) indicates that males mate with more than one female, and that females may go from male to male for breeding. However, Roberts (1956) reported observations from Transvaal of males and females, apparently pairs, of *I. minor* and of *I. indicator* (in which the sexes are clearly marked) acting in concert to enable the female to enter a host's nest. Thus, there may be a longer pair-bond than indicated by Friedmann (1955) and Ranger (1955).

The clutch size is four to as many as eight glossy, white eggs. The laying female usually breaks the hosts' eggs with her bill or oth-

erwise, during laying. Rarely (two cases) are two eggs laid in the same host's nest (Friedmann, 1955). Breeding occurs in the breeding period of the host species.

Eggs are known: in July from Gambia; April to June and August to December (encompassing one or both wet periods) in East Africa (Brown and Britton, 1980); July and September to October in Zambia (Benson et al., 1971); September to November and January for Zimbabwe (Stuart Irwin, 1981); September to October for Malawi (Benson and Benson, 1977); and September to January (mainly November–December) for Natal, South Africa. Reported breeding, based upon adults in breeding condition, or other indications are from: Gambia in July; Nigeria in January to July (Elgood, 1983); Cameroun in April; Sudan in March to April and October; Ethiopia in January to April; northern Zaire in January to May; southeastern Zaire in June, August, and October; Kenya in July and November; Tanzania in July to January; Angola in October; Zambia in September to October and March; Malawi in August to September and April; Zimbabwe from September to December; northern Mozambique in January; and South Africa, mainly from October to December, but also in September and January.

The very distinctive juveniles come from July and October to November (subadults) in Senegal; December in Ghana; April, June, and July (plus December subadult) in Nigeria; December and March in Cameroun; February (plus January to April subadults) in Sudan; February to April, June, and July, and August and September (plus December to March subadults) in Ethiopia; August to September, with a November subadult from Somalia; December and March, and June and August (plus subadults for March, July, and September) in Uganda; all months of the year in Kenya, with a concentration in December to February, May to July, and September to October; December, and February to July in Tanzania, with June and December subadults (in the dry periods); May to October in northern Zaire; January to March, May to July and December in southeastern Zaire (Upemba specimens); December to April and August, plus subadults in June and December (mainly in dry periods) in southern Zaire;

November, with November to January subadults in Angola; December and April in Zambia; December from Malawi; February, April and September from Mozambique; December from Zimbabwe; July and November from Botswana; and August to January and March, with subadults from November to May in Swaziland and South Africa.

The hatchling honeyguide (the incubation period is uncertain) is equipped with transparent bill hooks that overlap, and although the pinkish young are blind and featherless they bite any surviving young of the host, killing them. These hooks are lost at about 14 days of age (Friedmann, 1955; Ranger, 1955). The young honeyguide begs and receives food from the foster parents, remaining about 30 days in the nest. After leaving the nest the honeyguide calls loudly for food but does not follow the foster parents, nor does it return to the nest (Friedmann, 1955). There are few observations of feeding of fledged young, although they reportedly (Friedmann, 1955) are fed for up to 10 days after leaving the nest.

The independent young retain the yellow-breasted and yellow-throated plumage for some time, perhaps to six months of age. Subadults, that is birds in partly adult plumage, but retaining the traces of yellow below or (males) the blotchy black and white, or yellow, throat and blackish bill, may attempt to breed in this plumage (the golden wing mark, the fully black throat in males, and the pink bill in males, are the last colored areas to shift to the adult condition). Such subadults readily guide to honey sources. In their juvenal to subadult plumages young birds may gather in very loose feeding flocks about herds of cattle or game animals, the main instance of sociality exhibited in the species.

SUMMARY AND CONCLUSIONS

Data accumulated in the three decades since Friedmann's (1955) monograph still leave many unanswered questions about the Afrotropical honeyguides. Indeed, one gets the impression that we are on the verge of learning how these birds become independent, seek food, recognize conspecifics, spatially organize themselves, court, mate, select hosts, and lay in hosts' nests at the appropriate time.

The actual hosts are unknown for some honeyguides. In particular, the behavior and ecology of species of *Melichneutes* and *Melignomon*, somewhat intermediate morphologically between *Prodotiscus* and *Indicator*, are so little known that the evolution of extant honeyguides remains problematical. In addition, the biology of the smaller species (*willcocksii*, *pumilio*, *meliphilus*, and *narrowensis*) of *Indicator* is very poorly known.

The feeding of honeyguides is more open than ever for investigation, particularly the habits of locating and digesting wax. It is abundantly clear that honeyguides and honeybirds seek wax from one source (beeswax) or another (insects' exudates). How do they find wax and what part does it play in their diet? Our knowledge of honeyguide digestion can hardly be said to be solidly based, for the data are meager, and for but a few individuals of one species. Modern methods surely can lead quickly to breakthroughs in understanding the digestion of wax, and the nature of their seeming requirement for it. Honeyguiding itself, while intriguing, is far from universal, and indeed only one species (*I. indicator*) regularly guides—the honeyguides might be said to be misnamed, for "wax-birds" would appear to better reflect a trait common to many, if not all, of them.

A great deal has been accomplished in setting forth the hosts of the various honeyguides (although hosts are unknown for several species). We are at a point where we require more specific data. Does an individual female (or for that matter, males too) specialize in one host, or several? We have a list of hosts for some species, but only some indications of preferred hosts. There has been an emphasis on observers finding new hosts to add to the list for various honeyguides. It is time to concentrate more on the known, regularly used hosts, to ascertain their precise ecological interrelations with the parasitic honeyguides. Do preferred hosts vary from place to place, or even from season to season in the same locality? These and many other questions ought now to be posed, and answers sought, especially since some host species, and thus perhaps indirectly the honeyguides, are being affected adversely by human alteration of the African landscape on an ever grander scale.

One new thrust has been in the wealth of new information relating to honeyguides' behavioral relations with their hosts. These appear to be complex, at least in central and East Africa. The feeding of a young honeyguide by a conspecific adult (Brosset, 1981), and our observations of honeyguide activity about recently fledged young white-eyes accompanying their parents suggest that even in the honeyguides, the forming of pairs may be less brief and simple than has been thought. In the case of several species of *Indicator* there is considerable evidence that the honeyguides carefully monitor their hosts, their hosts' nesting and roosting sites, the nesting of the hosts, and the progress of the nesting even up to and beyond the point of fledging of the hosts' young, or of a young honeyguide. Young Lesser Honeyguides may see and certainly often hear adults, perhaps their parents, calling near them. Whether or not this plays a role in facilitating learning of vocalizations, or any imprinting effects remains to be established.

There is suggestive evidence from Lesser Honeyguides that part of the interplay between honeyguides and their barbet hosts beyond the period of egg-laying by the hosts may relate to disruption of the nesting effort, increasing chances of renesting, and thus providing another opportunity for the honeyguide to parasitize them. The number of times that two honeyguides have been seen about a host's nest strongly suggests cooperative actions that would enable the female to enter the host's nest. The seeking out of the barbets by a Lesser Honeyguide, eliciting chase after chase, may be a ploy to get the barbets from the nest to allow a female to enter. Males might even "play" at this to increase aggressive and chasing tendencies by the hosts at times other than while actually laying, to allow the drawing of the birds away from the nest at a later time (the host's habituation to the honeyguide, resulting in its failure to chase it, is the negative side of such activity to the honeyguide).

Until now there has been little appreciation of the aggressiveness of honeyguides intraspecifically, or with other species of honeyguides. The establishment of a dominance hierarchy based upon age and sex, at least at certain times and under certain conditions,

in Scaly-throated and Greater Honeyguides, is a new development bearing on aggression generally in honeyguides, and on territoriality. We are at present expanding our experiments to work with marked individuals. We hope to gain more information on how widespread the aggression is, and on the exact nature of the hierarchy under various conditions. It is possible that the behavior of conspecific honeyguides representing populations near the equator differs markedly from that of those from southern African populations. The latter are subjected to very strictly defined seasons limiting breeding, and, insofar as hosts vary, there are fewer choices of host species for southern honeyguides.

Only with our studies (1979) and the research of Chappuis (1981) has the analysis of honeyguide vocalizations really commenced. It appears that there are certain aggressive squeaky notes, trills, and chatters that have counterparts in several honeyguides. Of course the voices of some species are still unrecorded on tape, and indeed there is no vocal (or visual) display information available for a few honeyguides, so we are only beginning to evaluate such data for some species. One problem that emerges is that of the function and nature of song in the group. It appears that there are similarities in songs of many (e.g., *Indicator narokensis*, *I. willcocksi*, *I. exilis*, *I. conirostris*, *I. minor*, and even *I. indicator*) of the honeyguides, with those of *Indicator variegatus* and *I. maculatus* being divergent from others. The Lesser Honeyguide has an alternate song used more frequently in the tropics than is the primary song, which is so prevalent for much of the year in southern Africa. Correlated with this difference seems to be a difference in use and importance of singing perches in northern and southern regions. These differences may be related to the greater range of the breeding period and the monitoring of host species that seem notable in more northern birds, but has hardly been noted for the better known southern Lesser Honeyguides. Studies of the Thick-billed Honeyguide, a tropical forest species that sings virtually identically to the Lesser Honeyguide (to which it is very closely related, Friedmann, 1955), might aid in interpretation and understanding of the variation that seems to occur in the Lesser Hon-

eyguide. The problems of the precise relations among the taxa of *Prodotiscus*, and of the smaller species of *Indicator*, would be brought much closer to solution if we had access to data on their acoustic displays. In any case, greater knowledge of the form and function of honeyguide vocalizations is likely to help in understanding their apparently very complex biology.

In conclusion, we have made a number of advances in our knowledge of honeyguides. Their population dynamics, ecology, reproductive behavior, and foraging habits remain largely unknown. Even in areas of greatest progress (in establishing the identity of host species, in aspects of the activities of young honeyguides with their foster parents and the young of the latter, and in honeyguiding by one species), we can only be said to have arrived at the doorstep of a mist-enshrouded house whose form remains obscured. It is hoped that our studies, the updating of Friedmann's (1955) landmark work, and the summarizing we have attempted will stimulate further advances.

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